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THE APPLICATION OF NORMAL SOLUTIONS TO BIOLOGICAL PROBLEMS.

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JUDGING from recent investigations into the effects of ions upon plant and animal life, one is led to conclude that there is much confusion in regard to the interpretation of certain standard chemical solutions. It is not to be doubted that solutions have a very important part in biological functions, and because of their importance it is deemed advisable to attempt to place this branch of an important subject upon a firmer basis.

Since solutions of molecular concentration have been adopted for comparison, in place of the older percentage concentration solutions, there seems to be a great tendency to misinterpretation and confusion. Solutions prepared on the percentage basis are not now considered scientifically accurate when used for purposes of comparison, while those molecularly equivalent may be compared with scientific accuracy. The molecular and the equivalent solutions are the only ones here discussed.

Much of the physiological work done with molecular solutions proves upon examination to be faulty because of a misconception of the meaning of *normal* solutions, *gram-equivalent* per liter solutions, and *gram-molecule* per liter solutions. There are no less than three interpretations of what a normal solution is. One takes it to be a *gram-molecule* per liter of *solution*. Another takes it to be a *gram-equivalent* per liter of *solution*. Still another regards it as a gram-molecule or a gram-equivalent per liter of

water. Some use the symbol *n* (meaning in chemistry a normal solution) and say nothing about the method of preparation.

There are two probable causes for this confusion. The analytic chemists have differed in their use of solutions. (Allen, *Chem. News* **40**: 239; also *Analyst* **13**: 181, cited by Sutton **18**,[1] p. 28.) Some (a very few) German chemists use a gram-molecule per liter and call it a *normal* solution. By far the greater number of modern analytical chemists, however, use a *gram-equivalent* per liter of *solution* as a normal solution. The physical chemist uses both the above mentioned methods of preparation, but is always clear as to the meaning, and calls only the *gram-equivalent* per liter the *normal* solution. Those who use the chemical symbol *n* without explanation fall under some shadow of doubt arising from the above mentioned confusion. The work, however, may be faultless and the interpretation accurate. The theory of the separation, in aqueous solutions, of the molecules of compounds into ions is now a generally accepted one, and it is partly because of the actions of these ions, and of the dissociation of the molecule into ions, that there is great need of uniformity and of chemical accuracy in the preparation of solutions. Here are some definitions of *normal* solutions.

1. FRESENIUS (**2**, p. 687): "Solutions of such strength that 1000^{cc} contain an amount of acid or base equivalent to one gram of hydrogen are normal solutions, *e. g.*,

HCl,	mol. wt. 36.46,	wt. in	1000^{cc}	of solution	36.46
H_2SO_4,	" 98 ,	"	"	"	49
Na_2CO_3	" 106.08,	"	"	"	53.04"

Fresenius' chemical table (p. 846) is based on the above mentioned method of preparation.

2. SUTTON (**18**, p. 28): "Normal solutions are prepared so that one liter of solution at 16° C. shall contain the hydrogen equivalent of the active reagent in grams (H = 1)," *e. g.*:

[1] See bibliography at end.

HCl	1	mol. wt. in grams	per	liter	of solution
H_2SO_4	$\frac{1}{2}$	"	"	"	"
Na_3PO_4	$\frac{1}{3}$	"	"	"	"
$KMnO_4$	$\frac{1}{5}$	"	"	"	"
$K_2Cr_2O_7$	$\frac{1}{6}$	"	"	"	"(Talbot **19**, p.65)

3. TALBOT (**19**, p. 64): "A normal solution as defined by Mohr (Talbot **19**, pp. 64, 65) contains in one liter 'one equivalent of the active reagent in grams.' The equivalent in grams may be defined as 'that quantity of the active reagent which contains, replaces, unites with, or in any way, directly or indirectly, brings into reaction one gram of hydrogen.'"

MILLER and KILIKANI (**11**, p. 22), state regarding normality of solutions that "like volumes are equivalent to one another."

On the other side of the question, however, there are a few who use gram molecule per liter solutions and call them *normal* solutions. Of these, two perhaps are worth mentioning, Muter and Menschutkins, both cited by Sutton (**18**, p. 28).

In Ostwald's own work (**13**) he uses both gram-equivalent per liter and gram-molecule per liter of solution, but never confuses them. He uses the gram-molecule solutions for demonstrating molecular conductivity, and some of these tables are to be found in his Lehrbuch (**2**, pp. 722–772). Ostwald (**15**, p. 281) gives Kohlrausch's (**6**) table of equivalent quantities (not molecular quantities) for several solutions and enunciates the principle that the *equivalent* conductivity is a direct measure of the velocity of the migration of the ions. Ostwald (**14**, p. 284) uses normal solutions (with table) in regard to surface-tension of solutions, and on pp. 170–172 he uses *molecular* solutions with table of reference for molecular lowering of the vapor-pressure. There are only two instances of different tables used by Ostwald in his work. It will thus be seen that he makes use of both kinds of solutions according as they best suit his particular purpose.

Van't Hoff (**23**, p. 117), referring to Ostwald, uses the term "so-called molecular conductivity," and he uses freely the term normality as applied to solutions. Hittorf's table (Le Blanc **7**,

p. 78), is based on the *gram-equivalent* per liter solution, and Le Blanc (**7**, p. 79), uses the symbol λ to designate *equivalent* conductivity as distinguished from *molecular* conductivity, which is expressed by Ostwald as μ. Moreover, Valson's (**24**) law of the moduli (tables) is based upon gram-equivalent (not molecular) solutions, as well as almost all the analytical *chemical* tables now available.

It is seen that the physical chemist recognizes two kinds of standard solutions, *molecular* solutions and *equivalent* solutions, calling the latter *normal* solutions. The analytical chemist uses one kind of solution, the normal solution, *i. e.*, the gram-equivalent per liter solution.

The mistakes resulting from misinterpretation of *normal* solutions, and from a confusion of the terms *gram-equivalent* and *gram-molecule* per liter will be better understood if a few particular cases be cited. Kahlenberg and True (**5**, p. 85), speak thus: "Chemically equivalent quantities (*i. e.*, molecular quantities) of the different substances were not compared;" also (p. 91), "expressed in gram-molecules or gram-equivalents per liter;" showing that they regard a gram-molecule per liter as exactly the same as a gram-equivalent per liter, which, in the case of many of the substances referred to (*e. g.*, H_2SO_4), is not correct. What brings out more prominently the importance of the error is the fact that the solution of H_2SO_4 (p. 92) was a *normal* solution (purchased from the chemist), that is a gram-equivalent solution, and was thought to be a gram-molecule solution. Their results show that $\frac{1}{6400}$ gram-equivalent per liter of H_2SO_4 is as toxic as $\frac{1}{3200}$ gram-equivalent per liter of HCl. In other words, the experiments seem to prove that the solution of H_2SO_4 was what they *thought it to be*, though what *it was not*. Heald (**4**, p. 125), referring to Kahlenberg and True, states that "in these experiments the solutions were prepared according to gram-equivalents." On pages 119–123 of Kahlenberg and True we find written *gram-mol.* per liter.

Similar mistakes were made by True (**20**, p. 184), where he says, referring to H_2SO_4, "and since it splits off two hydrogen

ions from every molecule, it would have, in chemically equivalent quantities, twice the number of H ions found in HCl, and would have its death-limit at one half the concentration of the monobasic acid." This shows clearly that this author regarded chemical equivalent and molecular solutions as the same.

Kahlenberg and True (**5**, p. 6), say: "In the second column is the concentration just allowing growth, expressed in fractions of a gram-equivalent per liter of water." In the column referred to, the limit for H_2SO_4 is $\frac{1}{6400}$, and for $KHSO_4$ is $\frac{1}{6400}$ in equivalent solutions. Since the toxicity of potassium and of SO_4 at this concentration may be neglected (p. 6), the hydrogen in the $KHSO_4$ is as toxic as *twice* as much hydrogen in the case of H_2SO_4, since there is in chemically equivalent quantities of H_2SO_4 and $KHSO_4$ *twice* as much hydrogen in H_2SO_4 as there is in the $KHSO_4$.

Another instance of the error arising from confusing the gram-equivalent per liter with the gram-molecule per liter is shown in the work of Kahlenberg and True (**5**, p. 109). They say, referring to Ostwald (**16**), "the most dilute solutions with which he worked contained one gram-equivalent in 1024 liters." Ostwald's tables in this reference are *not* made on the gram-equivalent per liter plan, but on the *gram-molecule* per liter plan, and he so states (p. 174). "Die folgende Spalte enthalt unter 'm' den Wert der relativen molekularen Leitfähigkeit; der Wert von μ_∞, auf welchen derselbe bezogen ist, findet sich in der Ueberschrift der Tabelle angegeben." Also p. 171, "Wo μ_v die molekulare Leitfähigkeit bei der Verdünnung v (in Litern auf in Grammolekulargewicht), μ_∞ den Grenzwert derselben bei unendlicher Verdünnung und c eine Konstante bedeutet. Drückt man die molekulare Leitfähigkeit in Bruchtheilen ihres Grenzwertes aus, setzt also $m = \frac{\mu_v}{\mu_\infty}$."

Kahlenberg and True (**5**, p. 115) give in their tables 56, 57, 58, 59, "concentration gm.-equival. per liter," and refer to Ostwald (**16**, p. 380). Now Ostwald's tables (pp. 369–422) are made *not* on the plan gram-equivalent per liter but *gram-molecule*

per liter. No comment is necessary. Again Kahlenberg and True (**5**, p. 116), state, "as maleic acid at the dilution 1024 is dissociated 98.2 per cent. and fumaric acid 78.5 per cent., we should expect the latter to be less poisonous than the former if the toxic action be due to the H ions alone." In the table to which they refer we find maleic acid *92.8 per cent.* at 1024 and fumaric acid 78.5 at *2048*. They state further, referring to the two acids mentioned, "we do not place much reliance on the results obtained from these two acids as it is questionable whether the substances were perfectly pure." The discrepancy above referred to suggests another reason for unreliability of results.

True and Hunkel (**22**, p. 326), while using gram-molecule per liter in their paper, made reference to Kahlenberg and True (**5**, p. 92), where the tables are written gram-equivalent per liter. The one kind of table, of course, cannot apply directly to the other.

In regard to the method of preparation of solutions by dissolving a gram-equivalent of the salt, or a gram-molecule of the salt, as the case may be, in a liter of *water*, there is something to be said. Those who have made errors in this way are Pfeffer (**17**, p. 146), Detmer and Moor (**1**, p. 326), Kahlenberg and True (**5**, pp. 85, 87), True (**20**, pp. 184, 185), True (**21**, pp. 410, 411), Heald (**4**, p. 133), Garry (**3**, p. 298), True and Hunkel (**22**, p. 326), and Ostwald (**14**, p. 190). Pfeffer, Detmer and Moor, and Garry called them *normal* solutions. Kahlenberg and True called them gram-molecule solutions and gram-equivalent solutions, apparently interchangeably, but meaning generally molecular solutions. Ostwald is using Tammann's table which states that the solutions are made by dissolving *n* molecular weights, in grams, of the salts in 1000 grams of water.[2]

The objection to the above solutions is not so much to the

[2] MACDOUGAL (**10**, p. 51) says: "A normal solution of ethyl alcohol is made by adding 46 grams of absolute alcohol to a liter of distilled water." This, to be in any sense accurate, should read (after the word alcohol) *to sufficient water to make a liter of solution*. MacDougal's statement produces an error of about 58^{cc} in 1000^{cc}.

method of preparing them as to the application to them of chemical or physical tables prepared on a different basis; and to the error arising from their being called by names which mean something different. A solution prepared by dissolving one gram-equivalent in a liter of *water* is quite different in concentration (in the case of strong solutions especially) from that prepared by dissolving one gram-equivalent in a liter of *solution*. The difference is so apparent that explanation is unnecessary.

The use of the chemical symbol *n* to represent solutions without some explanation as to the method of preparation of the solution, is likely to cause some doubt to be cast upon the work. One will naturally infer that those who use the symbol without explanation are as likely to err as those who use it with explanation, but in making explanation show an error of interpretation; though this inference might be unfair.

Garry (**3**, p. 298) states: "To designate chemically equivalent solutions, the chemist uses fractional parts of the so-called *normal* solutions, *i. e.*, the solution made by dissolving the equivalent gram-molecule in one liter of water." He uses the symbol N to designate his solutions, but if he prepared them after the method indicted above he is not warranted in using the symbol for normal solutions. Chemical tables showing degree of dissociation will, of course, not apply to solutions so made.

True (**20**, p. 186) uses the term *n*-1024 in reference to Ostwald's tables (**16**), but he is not warranted in using this term because Ostwald's tables just referred to are *not* based on *normal* solutions but are molecular solutions. Heald (**4**, p. 138) uses the term *N* and refers to the same page of *Zeitschrift* for degree of dissociation. These tables do not apply.

In the works of Loeb (**9**), D. J. Lingle (**8**), and A. Moore (**12**) the symbol *n* is used to designate the solutions, but no explanation is given, though in the context there are indications that the symbol *n* is properly applied.

The results of the errors and misconceptions just referred to may be much or little according as the points brought out are of little or of much consequence. At all events, there seems need

of establishing this part of physiology upon a more secure and accurate basis. The analytical chemists and the physical chemists have done an enormous amount of investigation upon solutions, and they have established tables for various purposes. Their tables and results are convenient, clear, and ready for use; and the only way to make proper use of them is to make the solutions according to the chemist's standard.

Sutton (**18,** p. 28, footnote) gives a piece of excellent advice in the following statement: "Anyhow it is to be hoped that those who communicate processes to the chemical journals, or abstracts of foreign articles for publication, will take care to distinguish between the conflicting systems." If this advice is useful to the chemist, how much more useful should it be to those who are not chemists, but who in their work make use of tables of standard solutions made by the chemists.

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BIBLIOGRAPHY CITED.

1. DETMER and MOOR: Plant Physiology. 1898.
2. FRESENIUS: Volumetric Chem. Anal. 1884.
3. GARRY: The effects of ions upon the aggregation of flagellates. Amer. Jour. Physiol. **3**: 298. 1900.
4. HEALD: On the toxic effect of dilute solutions of acids and salts upon plants. Bot Gaz. **22**: 125. 1896.
5. KAHLENBERG and TRUE: On the toxic action of dissolved salts and their electrolytic dissociation. Bot. Gaz. **22**: 81. 1896.
6. KOHLRAUSCH and HOLBORN: Das Leitvermögen der Elektrolyte. 1898.
7. LEBLANC: Electro-chemistry. 1896.
8. LINGLE: The action of certain ions on ventricular muscle. Amer. Jour. Physiol. **4**: 265. 1900.
9. LOEB: On ion-proteid compounds and their rôle in the mechanics of life phenomena. Amer. Jour. Physiol. **3**: 327. 1900.
10. MACDOUGAL: Text-book of Plant Physiology. 1901.
11. MILLER and KILIKANI: Anal. Chem. 1891.
12. MOORE: Further evidence of the poisonous effects of a pure NaCl solution. Amer. Jour. Physiol. **4**: 386. 1900.
13. OSTWALD: Lehrb. d. Allg. Chem. II. ed. 2. 1893.
14. ———: Solutions (trans. by Muir). 1891.
15. ———: Outlines of Chemistry (trans. by Walker). 1895.

16. OSTWALD: Zeitschrift f. Phys. Chem. 3: 170, 241, 369. 1899.
17. PFEFFER: Plant Physiol. (trans. by Ewart). 1900.
18. SUTTON: Volumetric Analysis, ed. 7. 1896.
19. TALBOT: Introduction to Quantitat. Chem. Anal. 1899.
20. TRUE: The toxic action of a series of acids and of their sodium salts on *Lupinus albus*. Amer. Jour. Science. 9: 183. 1900.
21. ———: Physiological action of certain plasmolyzing agents. Bot. Gaz. 26: 407. 1898.
22. TRUE and HUNKEL: The poisonous effect exerted on living plants by phenols. Bot. Cent. 76: 9. 1898.
23. VAN 'T HOFF: Lectures on Phys. Chem. I. 1900.
24. VALSON: Compt. Rend. 73: 441. 1874.

GAMETOGENESIS AND FERTILIZATION IN ALBUGO.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXIX.

FRANK LINCOLN STEVENS.

(WITH PLATES I–IV)

[*Concluded from p. 169.*]

III. GENERAL CONSIDERATIONS.

OBSERVATIONAL evidence that kinoplasm and trophoplasm (Strasburger 1892) are true morphological elements of the cell has steadily increased, and striking experimental evidence has recently been adduced to confirm this conception (Hottes, *ined.*). In 1892 Strasburger proposed a theory of fertilization founded upon the assumption that sexual cells are incapable of development, owing to a kinoplasmic starvation. This theory was based partly upon observations on Ulothrix, and the relation of the cilia in sexual and asexual cells. Much confirmatory evidence has since been received, and in Strasburger's latest book (1900) the theory is developed more completely. As applied to sexually differentiated cells, the theory postulates kinoplasmic hunger in the female and trophoplasmic hunger in the male. The phenomena attending zonation in Albugo and Peronospora are capable of explanation in the light of Strasburger's theory, and in turn materially strengthen the theory itself. In Albugo and Peronospora the marshaling of the nuclei into a hollow sphere, a most conspicuous phenomenon, is quite inexplicable on the ground of atavism or phylogeny, nor can it have to do with wall-building. Why then do the nuclei habitually leave the ooplasm, apparently to perform no useful function in the periplasm, only to return and function as female pronuclei?

A study of the accompanying plates shows plainly that the periplasm is of a distinctly different character from the ooplasm.

The latter is typically very dense and alveolar, does not stain with gentian-violet but takes the orange G. The former stains darkly with the gentian-violet, and is filar, not alveolar. The processes leading to zonation may indeed be characterized provisionally as a differentiating of the oogonium into two regions, a periplasm rich in kinoplasm, and an oosphere rich in trophoplasm. This statement is borne out by all the positive characters of the trophoplasm and by the stain reaction and structure of the kinoplasm.

The nuclei are in mitosis and do not lose their membrane until zonation is sharp, nor do they reenter the ooplasm until their membrane is lost. The kinoplasmic nuclear membrane is apparently left in the periplasm, and its absence is evident during the second mitosis, thus resulting in that marked difference in character between the first and the second mitosis, which is illustrated in the figures, a difference which was noted in *A. Bliti* in my earlier paper (1899, p. 231). The nuclear membrane in the second mitosis is very thin or perhaps absent; the achromatic figure is weak and consequently often distorted and irregular. Every indication is that of an absence of kinoplasm.

Thus the behavior of both oogonial nuclei and cytoplasm confirms in a striking way the view that kinoplasm is important in sexual differentiation, and suggests that the nuclei pass to the periphery to rid themselves of superfluous kinoplasm, possibly to prevent parthenogenetic development in the oosphere. If this be the true reason for the migration of the nuclei, it logically follows that kinoplasm is not readily convertible into trophoplasm, at least not in the conditions that prevail in these oospheres.

In the antheridium a behavior complementary to that exhibited in the oogonium is seen. The antheridial protoplasm stains intensely with the gentian-violet before fertilization, but after fertilization the cytoplasm left in the antheridium fails to give this reaction. The antheridial nuclei as they lie in the tube possess a heavy membrane and stain darkly, giving every indication that they are rich in kinoplasm. In *A. candida* zonation is not

so marked, and the nuclei do not pass to the periplasm during division. In this species, however, there is a great preponderance of trophoplasm, owing to the highly developed coenocentrum, as well as to the fact that the trophoplasm of the whole oosphere is surrendered to one nucleus.

In general, the phenomena of oogenesis and spermatogenesis in Albugo afford remarkable confirmatory evidence for Strasburger's theory of fertilization. If the definite establishment of this theory should occur, botanists will come into more accord with those zoologists who accept the theory of Boveri that the sperm contributes the centrosome (kinoplasm), which is the one element needed by the egg to restore its capacity for division. Possibly the results of Klebs (1896), Loeb (1899), Nathansohn (1900), and others who have artificially induced parthenogenesis, may be explicable in the light of this theory, since it is at least conceivable that the environmental conditions which are supplied in these experiments may be identical with those which favor or retard the development of kinoplasm in the cell. Indeed, the results already attained by Hottes (1900) point in this direction.

No definite separating membrane can be detected in any of the species at the time of zonation, although the delimitation of periplasm and ooplasm is very sharp. Analysis of the condition shows that the differentiation is solely dependent upon the difference in character between the ooplasm and periplasm that has been described in previous paragraphs. It is outside of the ooplasm that the nuclei accumulate, and here in *A. Bliti*, *A. Portulacae*, and *A. Tragopogonis* they divide, some of the daughter nuclei returning to the oosphere.

The plasmoderma is formed at about the time that the primary oospheric nuclei renter, and at a period slightly later evidence of plasmolysis may be found. It appeared possible from some conditions seen in *A. Bliti* (Stevens 1899, *figs. 65–67*) that the nuclei might take some part in the formation of the new plasmoderma, but critical study shows that no constant relation is maintained between mitosis and plasmoderma formation. The

plasmoderma appears to arise directly from the cytoplasm in a manner closely resembling that which Mottier (1900) describes as a rearrangement of alveolar planes. The alveolae are here so small that it is impossible to assert with certainty that the processes are identical.

Simultaneous division of the nuclei in oogenesis and spermatogenesis is a phenomenon of wide distribution among the algae and fungi. The simultaneity itself is not remarkable, since it is frequently characteristic of multinucleate masses of cytoplasm, as endosperm nuclei of angiosperms, latex vessels (Pirotta and Buscalioni 1898), and plasmodia. The simultaneity in oogenesis is, however, of quite a different nature. Numerous vegetative nuclei, probably of very different ages, accumulate in the rudimentary sex organs and are there cut off from the parent cell. These nuclei pass simultaneously into mitosis, while the nuclei in the vegetative mycelium do not do so.[5]

This simultaneous mitosis, while it may be regarded with Hartog[6] (1891, p. 23) as a "phylogenetic reminiscence," is still often something more, and in the case of Albugo it is apparently a step necessary to the sexual differentiation of the gametes.

Whether a reduction in chromosomes occurs in connection with this gamete production is uncertain. To be sure Berlese (1898) claims to count the chromosomes during mitosis and fusion, and to establish definitely that reduction occurs in germination. The nuclear phenomena which he describes are so different from the conditions seen by Wager (1896), Davis (1900), and myself (1899), that the evidence must be accepted with reserve. The distinct difference in character between first and second mitosis in Albugo is, as I have said in another part of this paper, probably due to change in kinoplasmic content.

[5] Frequently nuclei in the immediate vicinity of the oogonium show a slight tendency to divide, and may even attain to the spirem stage (Stevens 1899, *fig. 45*).

[6] We can only regard the nuclear divisions in oogonium and antheridium as phylogenetic reminiscences of the formation of gametes by cell division; the periplasm is thus equivalent to a number of degenerate gametes which have taken on the function of epispore formation; the multitude of gametes are sacrificed to the few.

In three species of Albugo there are two mitoses, in another species probably two, in the gametangia; while in Peronospora (Wager 1900) there is only one. In Sphaeroplea (Klebahn 1899) the antheridial nuclei divide repeatedly, while the egg nucleus does not suffer visible change. In Vaucheria, even if there is a division in the oogonium, as seems possible (Oltmanns 1895, p. 392), it is probably not a differentiating division, since all of the nuclei but one wander back to the parent filament, and are presumably capable of vegetative function. From these examples it appears that the number of divisions in both oogenesis and spermatogenesis varies in different species, and differs in the two sexes of the same species; while in some forms there seems to be no mitosis directly concerned in the genesis of the female pronucleus. These conditions render improbable the existence of a reduction in the number of chromosomes during gametogenesis in these algae and fungi. Oogenesis and spermatogenesis begin almost simultaneously for a given pair or group of sex organs, yet all efforts to correlate their inception with any development external to the organs themselves were vain. A comparative study of four species shows no constant relation between the male and female organs in the sequence of their development, which seems to proceed independently in each organ. It is not probable, as might at first seem, that the inception of the antheridial tube is caused by the presence of the oosphere, since *fig. 50* presents a case where the antheridial tube grew and functioned normally, yet without a parallel development in the oogonium, or indeed the existence of an oosphere.

The factor which determines how many primary oospheric nuclei shall enter the ooplasm is uncertain. Clearly the position of the nucleus during its first mitosis determines whether or not one of the daughter nuclei shall enter the ooplasm. Yet this position seems to be governed by no law, the greatest irregularity existing, as is general in cases of simultaneous division in multinucleate masses of cytoplasm. This irregularity is equally prevalent at the time of zonation (*figs. 2, 28*). It is quite

possible, therefore, that mere accident determines how many of the nuclei are to be so oriented as to contribute daughter nuclei to the oosphere. It is needless to attribute to the cytoplasm any special selective power which causes definite nuclei or a definite number of them to return, although such selection is exhibited in some plants. For example, in the oogonium of Vaucheria (Oltmanns 1895) one nucleus maintains its position near the beak, amid violent activities of the surrounding cytoplasm, while the chloroplasts and numerous other nuclei are withdrawn. In the oogonium of Peronospora, according to Wager (1900), one nucleus of the many is selected to reenter the ooplasm and function as the female pronucleus.

The elimination of supernumerary nuclei by digestion in the surrounding cytoplasm finds analogy in vegetative cells in the sieve tubes of Pinus (Strumpf 1898); and still more striking in the sexual cells of Achlya (Trow 1899, p. 156), where there is an average of ten times as many nuclei as there are eggs to be produced. The phenomenon is also analogous to that described by Rückert (1892) and Oppel (1892), where several male nuclei enter the egg, the superfluous ones degenerating and functioning as yolk nuclei. In Actinosphaeria Hertwig (1898) also describes a reduction from multinucleate to uninucleate condition before fertilization, which is essentially similar to that seen in Albugo, the supernumerary nuclei being dissolved in the surrounding cytoplasm. In this species, as in Albugo, the nuclei are all alike, showing no such differentiation as is common among the infusoria. The phenomena seen in the Fucaceae (Oltmanns 1889), particularly in *Himanthalia lorea*, may be classed in this same category. Here the cytoplasm in early stages contains eight nuclei, the number being later reduced to one by casting off the seven superfluous ones.

In Vaucheria (Oltmanns 1895) the reduction from a multinucleate to a uninucleate condition is effected in quite a different manner, by protoplasmic streaming, the supernumerary nuclei being carried back into the parent hypha. Thus the reduction occurs before the oosphere is differentiated, and not in the

ooplasm proper. Klebahn (1899) describes in Sphaeroplea a case where the reduction from the multinucleate to the uninucleate condition does not occur until after fertilization, even if then, there being several nuclei in the oosphere only one of which is fertilized. The nuclei which receive no sperms are recognized in later stages by their smaller chromatin content, but their fate on germination was not followed. Golenkin (1900) agrees with Klebahn in finding a multinucleate egg, one nucleus of which functions; but Golenkin says that the nuclei then all fuse into one. Such a condition offers serious difficulties of interpretation in the light of the present theories regarding the cell. Since uninucleate oospheres were present among the multinucleate ones, it is possible that the condition observed by Golenkin was pathologic, a view which is strengthened by the fact that he was unable to germinate the spores after two years' trial.

In Saprolegniaceae Trow (1895, p. 630, and 1898, p. 166) notes a clumping or possibly pairing of the nuclei as they degenerate. I have also noted this phenomenon in the foregoing pages. Yet this is in no way to be confounded with the process of general fusion as described by Hartog (1891, p. 25) and Golenkin (1900), since these writers derive a functional nucleus from the ultimate result of successive fusions, while in the case observed by Trow, and in that seen by the writer, the nuclei thus appearing to fuse are really in the process of degeneration.

Inasmuch as it has been possible in all cases to follow the parallel development of the oospheres, it can hardly be doubted that in *A. Tragopogonis* and *A. candida*, as in Achlya, the Fucaceae, etc., the supernumerary nuclei represent potential pronuclei, and that each nucleus in the oosphere or *A. Tragopogonis* and *A. candida* is homologous with one of the nuclei in the oosphere of *A. Bliti* or *A. Portulacae*.

The coenocentrum has to some extent been discussed in connection with the description of *A. Tragopogonis* and *A. candida*. It yet remains to compare the structure in the different species. In *A. Portulacae* it is least developed, consisting simply

of a large zone of darkly staining cytoplasm which contains at its center the alveolar (trophoplasmic) region. This region seldom contains a globule such as characterizes the other three species. In *A. Bliti* the structure is much more prominent and endures for a longer period. It is of more complicated structure than in *A. Portulacae*, owing to the presence of a distinct central globule. In *A. Tragopogonis* the coenocentrum is still more highly developed. The central globule seems to be formed by the trophoplasm of the central region, or rather by the coalescence of the contents of its vacuoles. This globule in a later period becomes granular, the granules staining like nucleoli. *A. candida* possesses the most highly developed coenocentrum which, while closely resembling that of *A. Tragopogonis*, differs in that from its earliest formation till near the end of its functional activity it is thickly beset with coarse granules (*figs. 13, 17*) that in size and stain reaction agree with the nucleoli of this species.

In its function as well as structure this organ advances in complexity in the series here presented. In *A. Portulacae* there is no extensive accumulation of nutrient material in the vacuoles of the trophoplasm. In *A. Bliti* this accumulation is marked. In *A. Tragopogonis* the central globule shows strong chemotactic attraction for the nuclei and serves as nourishment for one or more of them. In *A. candida* this function of nutrition reaches greater perfection, as is shown by the attachment of the nuclei to the coenocentrum rather than their mere approximation to it. The coenocentrum develops earlier in the more highly differentiated species, and thus by exerting its attractive influence upon the nuclei before zonation strongly influences ontogeny. It has likewise probably been an important factor in changing the general character of oogenesis in phylogeny.

The presence of the receptive papilla in the four species of Albugo, as well as in Peronospora (Wager 1900, p. 270), attests to its importance either in the present or in ancestral species. Young stages in the development of this structure show that the plasmoderma adheres to the wall immediately under the

developing papilla, and exhibits a granular cytoplasm at this point. The granulation probably indicates the presence of a cellulose enzyme, formed here to soften the wall which alters chemically, as is evidenced by its response to stains and by its swollen condition (Stevens 1899, *figs. 47, 50*). The antheridial tube at this stage of development is probably unable to penetrate the cellulose wall of the oogonium, and that duty rests with the female cell.

Perhaps this curious structure can better be interpreted by a glance at possible ancestral forms. In algal aquatic forms, in which the gametangia open into the water, each sex organ opens independently, the female usually first. If the Peronosporeae have been derived from some such ancestors and these habits have been retained, in species where the walls of the antheridium and oogonium are in contact the origin of the receptive papilla is clear. Gametangia are usually of greatest turgor at the time of opening; therefore, in the present case the bulging, consequent upon the softening of the partition wall, is from the oogonium toward the antheridium. The formation of the receptive papilla in Albugo occurs immediately before the maturity of the oosphere, precisely as does the analogous phenomenon in Vaucheria.

The term "receptive papilla" is a misnomer, since this is not in any morphological sense a receptive structure, nor is it homologous with the receptive spot of the egg. In one case the differentiated area is part of an egg and functions as a place of reception for the sperm (as the eggs of Sphaeroplea, Saprolegnia, Oedogonium, etc.); in another case it is a zymogenic region of the protoplast adjacent to the point where an opening is to be made in an oogonial wall, either to furnish exit for the female gametes or for the entrance of the male elements, and is homologous with the opening spot of sporangia generally, as Cladophora, Bryopsis, Sphaeroplea, and Oedogonium. In the Saprolegniaceae the papilla does not furnish the place of entrance for the antheridium tube, although in Albugo it does (Zopf 1890, p. 293). The two regions occasion no danger of

confusion in the case of the multiovulate (vieleiig) oogonia, nor in cases where the egg is clearly differentiated in a surrounding periplasm; neither should they in forms like Vaucheria and Oedogonium.

The migration of antheridial nuclei into the tube seems to be independent of the developmental condition and metabolic activity of the oogonium, and is probably due to a negative rather than positive chemotropism, possibly of such a nature as that suggested by Hartog (1888) for the sporangia of the Saprolegniaceae. The objections raised by Humphrey (1892) to Hartog's view do not find application here, since he was considering cases where the sporangium failed to expel any of its spores. In Pyronema, where a condition similar to that of Albugo often prevails, Harper (1900, p. 362) explains the migration of some antheridial nuclei and the passivity of others by assuming that "the chemotactic or other stimulus which leads the male nuclei to migrate through the tube to the oogonium would in this case be assumed to have exhausted itself when a number equal to the number of egg nuclei had reached the oogonium." Such an hypothesis does not appear adequate for Albugo, for to assume that a stimulus which can arouse a given number of nuclei to migrate cannot bring the same activity to a greater number presents serious difficulties, and the supernumerary males are not found *en route*, as would be the case if they were stopped when the female nuclei have consorts and the hypothetical stimulating agent has been exhausted. The failure of some nuclei to leave the antheridium is more probably due to a lack of irritability on the part of some sperms than to a lack of the stimulating substance.

The phenomenon of the passage of nuclei from the body of the antheridium into its tube is no more comparable to the seeking of the female by a sperm than is the emptying of an algal sporangium, or an antheridium of the mosses or ferns, or the passage of the nuclei and cytoplasm from a pollen grain into the tube, all of which are clearly independent of chemotactic influence originating in organs of opposite sex, inasmuch as

they can occur in the entire absence of the female. It is after expulsion from the paternal gametangium that the chemotactic influence of the female unit is exerted upon the males. In the ferns, mosses, and most algae the chemotactic influence of the female extends over a comparatively wide region. In the spermatophytes the area is much restricted, since the pollen tube opens near the oosphere. In the Albuginaceae, where the male gametangium opens directly into the female gametangium, the region over which this influence may be exerted is still more limited. Indeed it may be questioned whether the force which brings the nuclei of the coenogametes (Davis 1900) together in pairs is at all the same as that which brings gametes together in the open. The pairing of nuclei in multinucleate masses of cytoplasm is comparable to the pairing of the male and female nuclei after the sperm has entered the cytoplasm of the egg, as is readily apparent from a consideration of the conditions presented in the larger eggs, as Fucus. Pfeffer demonstrated that the gametes in the open are drawn together by chemotactic attraction, and Wilson (1900) assumes that a similar attraction brings the nuclei together in the cytoplasm of the egg. Apparently two different forces operate, one to bring the sperm to the egg and induce penetration, the other to bring the pronuclei together in the ooplasm. Conklin (1899) has already distinguished these as distinct factors, and attempts to prove that in some cases at least cytoplasmic currents are responsible for the movement of the nuclei in the cytoplasm. Such an explanation does not seem adequate for the multinucleate oosphere of Albugo, as it would involve complexity inconceivably great. An explanation resting on chemotaxis is more tenable.

Conditions where an antheridial tube has reached the oosphere after that organ has been fertilized by another tube (*fig. 48*), as well as cases where two tubes open into one oosphere (*fig. 51*), show there is no correlation between the number of female nuclei to be fertilized and the number of nuclei which pass from the antheridial tube. This is also emphasized in *fig. 50*, where a tube is opening into an oogonium

having no oosphere, and into which an abundance of nuclei are poured. From these conditions, as well as direct observation, it is clear that the number of males and females is not exactly equal. In *A. Tragopogonis* unpaired male pronuclei are sometimes seen in the fertilized oosphere, but they are eventually digested by the ooplasm. Similarly, those male nuclei which do not pass into the antheridial tube, and those lying in an antheridium which forms no tube, fail to resume vegetative function and may be found *in situ* in stages of degeneration. The inability of such nuclei to function vegetatively attests their sexual differentiation and accounts for their subsequent rapid elimination.

One observation may help to disclose the force which directs the antheridial tube in its penetration of the oosphere. Two abnormal oospheres were seen quite devoid of nuclei. In one of these only the plasmoderma was developed (*fig. 52*), in the other periplasm and ooplasm were separated by a wall. In both cases the only antheridial tube present had gone astray in the periplasm. The absence of oospheric nuclei and the misdirection of the tube in the same oosphere may be only a peculiar coincidence.

Immediately after the opening of the antheridial tube a wall is seen surrounding the oospore. This develops with great rapidity, often attaining considerable thickness before the pronuclei have begun to fuse. Later thick walls, composed principally of cellulose for the nourishment of the germinating spore, are laid down from the inside, and on the outside heavy brown walls which are characteristically corrugated.[7]

In teratological forms, which abound in all species of Albugo, antheridial tubes where they lie in contact with the periplasm are frequently seen coated with the characteristic pectiniferous deposit. This occurrence was noted by DeBary (1863), and

[7] For brevity I shall hereafter use the term *pectiniferous* to designate this characteristic brown coating, inasmuch as pectin seems to be the constituent which is present here and absent from the other parts of the fungus. From the literature at hand the deposit appears to be really a mixture of cellulose, callose, cutin, and pectin, although its actual composition is yet open to question (Magnin 1895, Zalewski 1883).

mention of it is frequently found in works on the morphology of the group. Occasionally I have found isolated balls of this pectiniferous deposit lying in the periplasm. These observations in a measure confirm the generally accepted belief that the outer wall is laid down by the periplasm, a view originally proposed by DeBary (1863).

Sometimes an antheridial tube penetrates an oogonium that has not yet differentiated periplasm from ooplasm (*fig. 43*). In such case it often becomes coated with the characteristic pectiniferous wall of the species. More frequently it is aborted, reaching a length not greater than one-fifth the diameter of the oogonium. In such cases the adjacent oogonial walls and the remains of the aborted tube receive a pectiniferous coat (*figs. 44–46*). These phenomena tend to prove that undifferentiated cytoplasm of the oogonium has the ability to form the pectiniferous layer, and that in the absence of the plasmoderma of the oosphere it is apparently a matter of indifference what plasmoderma is to receive the deposit, although the pectin is laid down in contact with or by means of some plasmoderma or tonoplast in all cases.

Oogonia containing many small pectiniferous spheres (*fig. 46*) are quite frequently found, but the origin of the spheres cannot with certainty be determined. They are always accompanied by an aborted antheridial tube, and it may well be that these pectiniferous spheres represent deposits upon the lining membrane of vacuoles, thus emphasizing the similarity between the tonoplast and the plasmoderma in accord with the view of DeVries and Pfeffer. The fact that an aborted antheridial tube is present suggests that a stimulus may emanate from the antheridium which arouses the protoplasm to pectin production. This idea receives further support when it is recognized that the formation of the pectiniferous deposit begins and is most prominent near the antheridial tube (*fig. 44*). It thus often results in the tube becoming incrusted in a pectiniferous wall. *Fig. 45* represents an oogonium prematurely penetrated by two antheridial tubes from opposite ends. These tubes have aborted, but

each is accompanied by a pectiniferous formation from which the middle region of the oogonium is exempt.

Occasionally, by the formation of the oospore wall, a supernumerary antheridial tube is pushed aside in the periplasm. It then swells until it assumes a club-shaped appearance as it presses against the wall. In such cases the pectiniferous layer is formed over the whole mass, consisting of the mass of sperm nuclei and the remains of the antheridial tube (*fig. 48*). Conditions like these result, in the ripe spore, in a structure which looks much as though an antheridium lying beside an oospore had been encased (*fig. 49*). Such malformations may be distinguished from antheridia by the still persistent oogonial wall, which would of course not include the antheridium, but do include these masses.

If emanations from the antheridial tube stimulate the cytoplasm of the oogonium to form the pectiniferous layer, why does not the tube become coated as it penetrates the oosphere? This question probably receives its answer in the fact that the ooplasm has not the power to form pectin. It produces cellulose deposits, but not even in teratological cases (*fig. 47*) does it give evidence of any ability to form the pectiniferous layer. It is also notable that the ability to deposit the characteristic thick cellulose layer and to accumulate the typical oily globules is limited to the ooplasm. It seems, therefore, that in the activities leading to zonation there is a differentiation of the cytoplasm, that a capability vested in the oogonial cytoplasm is lost to the ooplasm, and its manifestation in later stages becomes limited to the periplasmic regions.[8] Whether this differentiation consists merely in a shifting of partially elaborated products of metabolism or in a segregation of living cytoplasm into two regions, one possessing a different constitution from the other, must be left an open question.

The stimulating effect from the antheridium may be manifested when the tube has penetrated only half way to the center

[8] The figures of Magnin (1895, *fig. 11*) might at first glance appear to contradic this, but Magnin's figures represent callose which is really present both in inner and outer walls.

of the oosphere without emptying, the stimulating agent presumably passing through the wall of the tube when this becomes very thin. The conditions justify the hypothesis that the protoplasm of the oogonium, or the periplasm as the case may be, contains the food constituents needed for the rather extensive production of the pectiniferous deposit, and that the substance contributed by the antheridial tube is more properly comparable to an enzyme than a food. It is a stimulant to activity rather than a material to act or to be acted upon. The protoplasm of the antheridium of Albugo, moreover, seems never to produce pectin, thus favoring the hypothesis that the necessary food materials are limited to the protoplasm of the oogonium.

The antheridial tube in normal conditions opens near the center of the oosphere, from whence the stimulating agent diffuses outward, awakening no response in the ooplasm because this is incapable of response. When this stimulating agent reaches the oospheric plasmoderma it meets the periplasm, which immediately lays down the rudiment of the outer wall. The fact that the tube opens in the center of the oosphere explains the absence of pectin formation in the periplasm, since the large area of the oospheric plasmoderma is ample to receive all the pectin that is to be laid down. Moreover, the thickening wall probably retards the passage of the stimulating agent into the periplasm, so that the peripheral portion of the periplasm is not incited to formation of the pectiniferous layer, and therefore the oogonial wall receives no pectiniferous coat. An answer to the question originally propounded by Cornu (1872) "si ce plasma extérieur a la propriété de se déposer en couche membraneuse, sans être élaboré au préabable, pourquoi ne se dépose-t-il pas aussi sur les parvis d l'oogone?" is thus suggested.

Normally it is the periplasm that responds to the stimulus, and the periplasm is bounded by its own plasmoderma and contains its own nuclei. It is an independent unit distinct from the oosphere, although it is destined to sacrifice itself for the protection of the oospore in a manner analogous to the tapetal

cells in many pteridophytes (Strasburger 1889). Normally, therefore, the production of pectin in Albugo is analogous to the so-called secondary effects of fertilization commonly seen in the higher plants, since it is an effect manifested by a cell other than those directly concerned in the act of fertilization.

SUMMARY OF SECTIONS II AND III.

The processes leading to zonation may be regarded as the differentiation of an ooplasm rich in trophoplasm. The nuclei pass outward, possibly to leave part of their kinoplasm outside of the ooplasm, in order to lessen the possibility of parthenogenetic development. The antheridial nuclei give evidence of heightened kinoplasmic content.

The cell plate is formed, without the participation of the nuclei, by a rearrangement of alevolar planes.

The simultaneous mitosis in gametogenesis is a phylogenetic reminiscence, and was of value in ancestral forms in increasing the number of gametes.

No constant time relation is maintained between the phases of oogenesis and spermatogenesis, but each after its inception seems to proceed independent of the other.

The orientation of the nuclear figure determines which, and consequently how many, primary oospheric nuclei shall enter the oosphere. This orientation seems to be merely accidental.

The supernumerary nuclei are phylogenetically gametes, and their dissolution finds analogy in the Saprolegniaceae and Fucaceae, in Actinosphaeria, and in cases of physiological polyspermy.

The receptive papilla is the result of a softening of the oogonial wall by the oogonial contents, accompanied by high turgor in the oogonium. It is probably a vestigial character recalling an algal ancestry. It is a structure of the oogonium, and therefore is not homologous with the receptive spot, which is a differentiated region of the oosphere.

The migration of the sperms from the antheridium is homologous with the emptying of a sporangium, rather than with

the seeking of the female by a male. The number of antheridial nuclei which migrate into the oosphere bears no constant relation to the number of waiting female nuclei. The failure of some nuclei to leave is probably due to a lack of irritability.

Superfluous nuclei of either sex which cannot resume vegetative function degenerate.

The periplasm has the ability to form the pectiniferous deposit, but the differentiated ooplasm cannot. Emanations from the antheridial tube seem to be needed to stimulate the ooplasm to this activity. The pectiniferous layer is deposited on or by a plasmoderma or tonoplast.

The four species, *A. Portulacae*, *A. Bliti*, *A. Tragopogonis*, and *A. candida* constitute a series in which the coenocentrum increases in complexity, the receptive papilla decreases, and the number of functional nuclei decreases. Of these *A. Portulacae* is probably the most primitive, and *A. candida* the most highly specialized form.

The coenocentrum was an important factor in evolution from the multinucleate to the uninucleate condition of oosphere.

The division of the fusion nucleus before passing to the winter condition is a consequence of the uninucleate condition, and constitutes the initial step in germination.

Delay in the division of the fusion nucleus in a uninucleate oospore is associated with retarded and slow fusion of the sexual nuclei, and is explicable as a consequence of slowness in completion of the last steps of fusion.

The relation between Albugo, Peronospora, and Saprolegnia is emphasized by their cytological character, and all are probably derived from a common ancestor having a multinucleate oosphere. The derivation of Peronospora and Saprolegnia from the Chytridineae is rendered improbable.

Pythium is more closely related to the Albuginaceae than to the Saprolegniaceae.

The peripheral gathering of the protoplasm in the oogonium of Saprolegnia may indicate closer relation to Peronospora than to Albugo.

If the Phycomycetes are related to Vaucheria it is from a period before the attainment of the uninucleate oosphere by Vaucheria.

The coenogamete is homologous with some or all of the gametes of a plurigametic gametangium, not with the individual gametes of such a structure.

There is a remarkable agreement between Albugo and Pyronema in many details.

The coenogamete is a result of pushing the synplast habit from the vegetative body into the reproductive organs.

The synplast of the Phycomycetes is a unit in both morphological and physiological sense, although it is philogenetically the equivalent of many units.

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BIBLIOGRAPHY.

ARTARI, 1890: Zur Entwickelungsgeschichte des Wassernetzes. Bull. de la Soc. Impér. des Naturalistes de Moscou, No. 2.

BERLESE, 1898: Ueber die Befruchtung und Entwickelung der Oosphäre bei den Peronosporeen. Jahrb. f. wiss. Bot. **31**: 159–196.

BERTHOLD, 1880: Die geschlechtliche Fortpflanzung von *Dasycladus clavaeformis* Ag. Bot. Zeit. **38**: 648–651.

BLACKMAN, 1900: The primitive Algae and the Flagellata, an account of modern work bearing on the evolution of the Algae. Ann. Bot. **14**: 647–688.

CHIMIELEWSKY, 1889: Zur Frage über die Copulation der Kerne beim Geschlechtsprocess der Pilze. Arbeiten d. neurussichen Naturf.-Gesselschaft **13**: 113.

CONKLIN, 1898: Protoplasmic movement as a factor of differentiation. Biol. Lect. at Woods Hole 17–43.

CORNU, 1872: Monographie des Saprolégniées. Ann. Sci. Nat. Bot. V. **16**: 5–198.

DANGEARD, 1890: Recherches histologiques sur les champignons. Le Botaniste **2**: 125.

DAVIS, 1899: The spore mother cell of Anthoceros. Bot. Gaz. **28**: 89–108.

— 1900: The fertilization of *Albugo candida*. Bot. Gaz. **29**: 297–310.

DE BARY, 1863: Recherches sur le développement de quelques champignons parasites. Ann. Sci. Nat. Bot. IV. **20**: 14.

— and STRASBURGER, 1877: *Acetabularia mediterranea*. Bot. Zeit. **35**: 713–728.

—— 1881 : Zur Kenntniss der Peronosporeen. Bot. Zeit. **39** : 617–625.

—— 1884 : Vergleichende Morphologie und Biologie der Pilze, Mycetozoen und Bacterien.

DRÜNER, 1895 : Studien über den Mechanismus der Zelltheilung. Jenaische Zeitsch. **29** : 2.

FISCHER, 1892 : Phycomycetes. Rabenhorst's Kryptogamenflora IV.

GOLENKIN, 1900 : Algologische Mittheilungen. Ueber die Befruchtung bei *Sphaeroplea annulina* und über die Structur der Zellkerne bei einigen grünen Algen. Bull. Soc. Imp. Nat. Moscow **1899** : 343.

HABERLANDT, 1896 : Physiologische Pflanzenanatomie. [2d ed.]

HANSTEIN, 1880 : Botanische Abhandlungen. **4** : —. [part 2.]

HARPER, 1900 : Sexual reproduction in *Pyronema confluens* and the morphology of the ascocarp. Ann. Bot. **14** : 321–400.

HARTOG, 1888 : Recent researches on the Saprolegniaceae, a critical abstract of Rothert's results. Ann. Bot. **2** : 201–216.

—— 1891 : Some problems of reproduction. Quart. Jour. Micr. Sci. **33** : 1–79.

—— 1895 : On the cytology of the vegetative and reproductive organs of Saprolegniaceae. Trans. Roy. Irish Acad. **30** : 649.

HERTWIG, 1892 : Die Zell und die Gewebe.

—— 1898 : Ueber Kerntheilung, Richtungs-Körperbildung und Befruchtung von *Actinosphaerium Eichorni*. Abhand. bayer. Akad. Wiss. **19** : —. [part 3.]

HUMPHREY, 1892 : The Saprolegniaceae of the United States, with notes on other species. Trans. Ann. Phil. Soc. **17** : 63–148.

ISTVÁNFFI, 1895 : Ueber die Rolle der Zellkerns bei der Entwickelung der Pilze. Ber. d. deut. bot. Gesells. **13** : 456.

IWANOFF, 1898 : Zur Entwickelungsgeschichte von *Botrydium granulatum* Woron. et Rostaf. Soc. Imp. Nat. St. Petersburg. Compt. Rend. —: 155.

JORDAN, 1893 : The habits and development of the newt. Jour. Morph. **8** : 269–366.

KLEBAHN, 1899 : Die Befruchtung von *Sphaeroplea annulina* Ag. Festschrift für Schwendener 81–103.

KLEBS, 1896 : Die Bedingungen der Fortpflanzung bei einigen Algen und Pilzen.

KOHL, 1897 : Zur Physiologie des Zellkerns. Bot. Centralb. **72** : 168.

KORSCHELT, 1889 : Beiträge zur Morphologie und Physiologie des Zellkernes Zool. Jahrb. Abt. für Anat. und Ontog. der Thiere **4** : —.

LAGERHEIM, 1899 : Mykologische Studien. II. Untersuchungen über die Monoblepharideen. Meddelanden från Stockholms Högskola no. 199. Bihang till Kongl. Svenska Vetenskaps-Akademiens Handlingar **25** : 42.

LOEB, 1899 : On the nature of the process of fertilization, etc. Am. Jour. Phyiol. **3** : 135.

MAGNIN, 1895: Recherches anatomiques sur les Péronosporées. Bull. Soc. Hist. d'Autun **8**: 3–56.

MOTTIER, 1900: Nuclear and cell division in *Dictyota dichotoma*. Ann. Bot. **14**: 163–192.

MUNSON, 1898: The ovarian egg of Limulus. Jour. Morph. **15**: 2.

NATHANSOHN, 1900: Ueber Parthenogenesis bei Marsilia und ihre Abhängigkeit von der Temperatur. Ber. d. deut. bot. Gesell. **18**: 99–109.

NOLL, 1888: Die Wirkungsweise von Schwerkraft und Licht auf die Gestaltung der Pflanze. Naturwiss. Rundschau **3**: 57.

OLTMANNS, 1889: Beiträge zur Kenntniss der Fucaceen. Abhand. Gesam. Bot. **14**: 1–94.

—— 1895: Ueber die Entwickelung der Sexualorgane bei Vaucheria. Flora **80**: 388–420.

—— 1898: Die Entwickelung der Sexualorgane bei *Coleochaete pulvinata*. Flora **85**: 1–14.

OPPEL, 1892: Die Befruchtung des Reptiliensies. Archiv. f. mikr. Anat. **39**: 215–216. *pls. 9–12*.

PFEFFER, 1897: Pflanzenphysiologie. [2d ed.]

PIROTTA and BUSCALIONI, 1898: Sulla presenza di elementi vascolari multinucleati nelle Dioscoreaceae. Ann. R. Inst. Bot. Roma **7**: 237–254.

RAUWENHOFF, 1888: Recherches sur le *Spaeroplea annulina* Ag. Arch. Néerland sc. exact. et nat. **22**: 91–144.

ROSTAFINSKI und WORONIN, 1877: Ueber *Botrydium granulatum*. Bot. Zeit. **35**: 649-664.

RÜCKERT, 1892: Ueber phyisologische Polyspermie bei meroblastischen Wirbelthiereiern. Anat. Anzeiger **7**: 320–333.

SCHRÖETER, 1893: Mucorineae. Die natürlichen Pflanzenfamilien **1**[1]: 119.

STEVENS, 1899: The compound oosphere of *Albugo Bliti*. Bot. Gaz. **28**: 149.

STRASBURGER, 1880: Zellbildung und Zelltheilung. [3d ed.]

—— 1889: Ueber das Wachsthum vegetabilischer Zellhäute. Hist. Beiträge **2**: 1–186.

—— 1892: Schwärmsporen, Gameten, pflanzliche Spermatozoiden, und das. Wesen der Befruchtung. Hist. Beiträge **4**: 48–158.

—— 1893: Ueber die Wirkungssphäre der Kerne und die Zellgrösse. Hist. Beiträge **5**: 97–124.

—— 1897: Ueber Befruchtung. Jahrb. f. wiss. Bot. **30**: 406–422.

—— 1900: Ueber Reductionstheilung, Spindelbildung, Centrosomen und Cilienbildner im Pflanzenreich.

STRUMPF, 1898: Zhistologii sosny (Zur Histologie der Kiefer). Anzeiger Akad. Wiss. Krakau.

TROW, 1895: The karyology of Saprolegnia. Ann. Bot. **9**: 609–652.

—— 1899: Observations on the biology and cytology of a new variety of *Achlya Americana*. Ann. Bot. **13**: 131–179.

VERWORN, 1897: Allgemeine Physiologie. [2d ed.]

WAGER, 1896: On the structure and reproduction of *Cystopus candidus*. Ann. Bot. **10**: 295–342.

—— 1900: On the fertilization of *Peronospora parasitica*. Ann. Bot. **14**: 263–273.

WILSON, 1900: The cell in development and inheritance.

ZALEWSKI, 1883: Zur Kenntniss der Gattung Cystopus. Bot. Centralb. **15**: 1–10.

ZIMMERMANN, 1896: Die Morphologie und Physiologie des pflanzlichen Zellkernes.

ZOPF, 1890: Die Pilze in morphologischer, physiologischer, biologischer und systematischer Beziehung. Schenk's Handbuch der Botanik **4**: 271–756.

EXPLANATION OF PLATES I–IV.

All figures are from material killed in chrom-acetic acid and stained with Flemming's triple stain. The figures were sketched with the aid of an Abbé camera, using the Leitz $\frac{1}{16}$ objective, aperture 1.30, and oculars 1 and 4.

PLATE I. Albugo Portulacae.

FIG. 1. Early stage in massing of protoplasm; nuclei in advanced prophase; receptive papilla prominent. × 857.

FIG. 2. Later stage in oogenesis; nuclei near metaphase; ooplasm and periplasm of very different structure, but not sharply delimited. × 857.

FIG. 3. Zonation; nuclei in metaphase; ooplasm and periplasm sharply differentiated; coenocentrum prominent, consisting of a loosely vacuolate center surrounded by a denser, slightly granular region which stains darker with the orange G. × 857.

FIG. 4. Slightly later than *fig. 3*; primary oospheric nuclei entering oosphere; ooplasm and periplasm sharply delimited; ooplasm typically alveolar, staining very lightly with orange G; periplasm staining densely with gentian violet, filar in structure; three reentering nuclei show each a very weak but distinct polar ray; coenocentrum has disappeared. × 857.

FIG. 5. Primary oospheric nuclei before second division; receptive papilla very prominent; later than *fig. 4*. × 857.

FIG. 6. Receptive papilla open; oospheric nuclei in second mitosis. × 857.

FIG. 7. Antheridial tube in oblique section showing many nuclei and no walls; oospheric nuclei in second mitosis. × 857.

FIG. 8. Antheridial tube in section slightly oblique; sperm nuclei numerous, elongated; stage slightly older than in *fig. 7*. × 1366.

FIG. 9. Transverse section of the antheridial tube, showing its multinucleate character. Oosphere of about the age shown in *fig.* 7. × 1366.

FIG. 10. Nuclei pairing after opening of antheridial tube, a distinct wall surrounding oospore; remains of antheridial tube visible in periplasm; degenerating nuclei in antheridium. × 857.

FIG. 11. Fusion complete; stage before accumulation of oils and before the outer walls are complete. × 857.

FIG. 12. Portion of mature wall. × 857.

PLATE II. Albugo Candida.

FIG. 13. Very young coenocentrum showing that the granules pass in from the surrounding ooplasm; oosphere slightly younger than stage next shown. × 1366.

FIG. 14. Early oogenesis; oosphere roughly outlined by a withdrawal of the protoplasm from the oogonium wall, leaving only a loose periplasm behind; nuclei approximately in metaphase; coenocentrum well developed. × 1366.

FIG. 15. After first division; several nuclei clustered around the coenocentrum; some already gone to the periplasm. × 1366.

FIG. 16. Later than *fig. 15;* nearly all of the nuclei have retreated to the periplasm; those remaining in the ooplasm in mitosis. × 1366.

FIG. 17. Later than *fig. 16;* mitosis complete. × 1366.

FIG. 18. Very slightly later than *fig. 13;* nucleus in metaphase, elongated owing to attraction by coenocentrum; coenocentrum densely and coarsely granular. × 1366.

FIG. 19. Two nuclei attached to coenocentrum; one in late anaphase, the other in telophase; coenocentrum more dense than in *fig. 18;* oosphere similar to that shown in *fig. 14.* × 1366.

FIG. 20. Similar to *fig. 19;* one nucleus in late anaphase attached to coenocentrum. × 1366.

FIGS. 21, 22. One nucleus much enlarged attached to coenocentrum by a pseudopodium-like extension; all other nuclei lie in the periplasm. × 1366.

FIG. 23. Before fusion; male and female nuclei and a supernumerary nucleus near the coenocentrum. × 1366.

FIG. 24. Metaphase of first division of fusion nucleus. × 1366.

FIG. 25. Anaphase of first division of fusion nucleus. × 1366.

FIG. 26. An antheridial tube bearing two nuclei; the female nucleus lying in the ooplasm near the coenocentrum. × 1366.

PLATE III. Albugo Tragopogonis.

FIG. 27. Early stage of oogenesis; protoplasm collected in one central mass; nuclei approaching metaphase; a slight indication of the coenocentrum apparent in the center. × 857.

FIG. 28. Condition slightly later than *fig. 27*; oogonium just before zonation; nuclei approximately at metaphase in both oogonium and antheridium; no sharp separation between ooplasm and periplasm. × 857.

FIG. 29. Slightly later than *fig. 28*; anaphase of first division; daughter nuclei entering ooplasm; ooplasm and periplasm sharply differentiated. × 1366.

FIG. 30. Immediately after the first division; primary oospheric nuclei moving toward coenocentrum, two of them strongly elongated; differentiation between ooplasm and periplasm sharp; plasmoderma probably present and many periplasmic nuclei pressing against it; coenocentrum prominent. × 857.

FIG. 31. Slightly later than *fig. 30*; ooplasm and periplasm separated by definite plasmoderma; oosphere multinucleate; coenocentrum contracted to a spherical homogeneous globule surrounded by dense protoplasm; primary oospheric nuclei attracted by coenocentrum. × 857.

FIG. 32. Metaphase of second mitosis; several nuclei attached to the coenocentrum; periplasmic nuclei not dividing; plasmoderma well defined; coenocentrum staining darkly and not homogeneous. × 857.

FIG. 33. Antheridial tube nearly ready to open, bearing several nuclei; oosphere in same condition as shown in *fig. 32*, *i. e.*, nuclei in second mitosis. × 1366.

FIG. 34. Similar to *fig. 32*; nuclei in second anaphase; ten dividing nuclei discernible in this one section. × 857.

FIG. 35. One female nucleus lying beside the coenocentrum—somewhat larger than daughter nuclei of second division; general appearance of the oosphere much like that in *fig. 36*. × 1366.

FIG. 36. After the opening of the antheridial tube; definite wall surrounding oosphere; remains of antheridial tube in oosphere; female nucleus in resting condition much larger than in *fig. 35* and lying beside the remains of the coenocentrum, which has lost its characteristic form; sperm nucleus somewhat elongated. × 857.

FIG. 37. Male and female nuclei lying in contact, both in resting condition, enveloped by the remains of coenocentrum; male larger than in earlier stages; compare *figs. 35, 36*. × 1366.

FIG. 38. Similar to *fig. 37*; also showing degenerate nuclei from same oosphere. × 1366.

FIG. 39. Fusion nucleus and remains of coenocentrum. × 1366.

FIG. 40. Anaphase of first division of fusion nucleus. × 1366.

FIG. 41. Winter condition of spore, showing thirteen nuclei in one section. × 857.

FIG. 42. Receptive papilla; oosphere like that shown in *fig. 32*.

PLATE IV. Teratological forms from various species (× 1366 or 857, and slightly reduced in reproduction).

FIG. 43. Antheridial tube penetrating oogonium in which no oosphere has been differentiated; tube branched and heavily coated with pectin; pectin also on oogonial wall in neighborhood of antheridium. *A. Tragopogonis.*

FIG. 44. Oogonium in which no oosphere was developed; antheridial tube small; deposit of pectin on oogonial wall in neighborhood of antheridium; also isolated pectin deposits, presumably in vacuoles; large deposit on the remains of the antheridial tube. *A. Portulacae.*

FIG. 45. An oogonium similar to that shown in *fig. 44;* two antheridia in contact with an oogonium; deposits of pectin lining the walls and projecting into the oogonium in the neighborhood of the antheridium; isolated balls of pectin lying free in the oogonium. *A. Portulacae.*

FIG. 46. An oogonium which developed no oosphere; masses of characteristic pectin distributed through the oogonium; deposits of pectin on the oogonial wall adjacent to the antheridium. *A. Portulacae.*

FIG. 47. Teratological formation of inner wall; redrawn from sketch, slightly diagrammatic. *A. Bliti.*

FIG. 48. Antheridial tube lying against plasmoderma of an oosphere fertilized by another antheridium; oosphere showing five nuclei in this section; antheridial nuclei in dense cytoplasm in the extreme tip of the tube; pectin formation encasing both oosphere and the end of the tube of the supernumerary antheridium. *A. Portulacae.*

FIG. 49. Similar to *fig. 48;* an older condition, showing whole structure surrounded by the remains of oogonial wall. *A. Portulacae.*

FIG. 50. Antheridial tube opening into an oogonium which has developed no oosphere; many male nuclei passing out, tube cut slightly oblique. *A. Portulacae.*

FIG. 51. Two antheridial tubes, each bearing many nuclei, opening simultaneously into one oosphere; one in transverse, one in longitudinal section. *A. Bliti.*

FIG. 52. Oosphere fully differentiated and devoid of nuclei; antheridial tube astray in periplasm; periplasm and antheridium normal. *A. Bliti.*

FIG. 53. An oogonium containing two coenocentra; oosphere bilobed, one coenocentrum lying at the center of each lobe; metaphase similar to *fig. 26. A. Tragopogonis.*

THE ECOLOGICAL RELATIONS OF THE VEGETATION OF WESTERN TEXAS.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXX.

WILLIAM L. BRAY.

(WITH TWENTY-FOUR TEXT FIGURES)

[*Concluded from p. 217.*]

SEMI-XEROPHYTIC FOREST OF THE HIGH MOUNTAIN SUMMITS AND WATERED CANONS OF TRANS-PECOS TEXAS.—On the higher Guadalupe and Davis mountains the annual rainfall is several inches greater than the normal for that meridian, and greater than in similar altitudes in the mountains of the Great bend of the Rio Grande. The mean temperature also, because of the northerly position and altitude, is enough lower than in other portions of trans-Pecos Texas to make these mountain summits a distinct zone, namely the Transition zone. On these higher summits and in the well-watered cañons leading down from them, the extreme xerophytic conditions of the region are very much modified. This becomes very evident in the aspect of the prevailing formation, an almost mesophytic forest.

The chief elements of the formation are as follows: *Pinus ponderosa*, on Guadalupe peak at 9000 feet, attains a height of 50 feet, with trunk 2 feet in diameter; on the Davis mountains it has yielded clear lumber 18 inches wide. This is the prevalent species, occurring in places in pure formation, as at the "pinery" northeast of Limpio peak. Next in prevalence is *Pseudotsuga taxifolia*, which attains similar dimensions. *Pinus flexilis* reaches a diameter of scarcely more than a foot. Below there begin *Pinus edulis*, *Juniperus pachyphloea*, and the oaks of the xerophytic slopes. The summit formation descends into the upper cañons a short distance.

In addition to the species just cited, the following transition

species are important elements: *Cercocarpus parvifolius*, *Ribes viscosissimum*, *Fendlera rupicola*, *Frasera speciosa*, *Geranium caespitosum*, *Campanula rotundifolia*, *Heuchera rubescens*, *Artemisia frigida*, and *Acer grandidentata*. A few of these reach the summits of the highest mountains in the Great bend, but scarcely in force enough to change the strongly upper Sonoran character.

FIG. 14.—Vegetation of adobe slopes and chalk exposures: characteristic of Cretaceous Texas, especially on the Grand prairie and the eastern half of the Edwards plateau.

In the lower cañons, the dwarfed arborescent species of the xerophytic slopes become large trees of regular symmetrical growth. Thus, *Quercus Emoryi* "becomes a straight tree 2 to 4 feet in diameter and 60 feet tall, forming the main feature of the sylva. Here also *Pinus edulis* attains the unusual size of 18 inches in diameter and 40 feet in height" (Havard). These cañons contain in addition numbers of characteristically mesophytic or semi-mesophytic woody species, as species of Prunus, Acer, Philadelphus, and Fendlera, while the sides of watered

cañons and the bottoms of dry ones contain those species of the central erosion formation whose range is to the southwest and west. In the main, however, the dry cañons and lower slopes are beset with a chaparral formation, to be discussed separately

XEROPHYTIC AND SEMI-MESOPHYTIC POST OAK FORMATIONS.—The post oak formation furnishes a striking instance of the close relation existing between soil structure and its vegetation covering. Where there are exposures of coarse sand beds and gravelly clays, at least as far west as the 100th meridian, there occurs an arborescent formation whose main elements are the two species of oak *Quercus minor* (post oak) and *Q. Marilandica* (black jack). Very extensive areas of this formation occur also on the western margin of the east Texas forest belt. In the west Texas region the areas are in the main as follows: (1) the extension of Fayette sands into the Rio Grande plain; (2) the gravelly débris and sands of the granitic area and its borders (extending for example westward beyond Fredericksburg); (3) the sands and gravels of the Carboniferous area (Brownwood and Palo Pinto countries); (4) the upper cross timbers (the lower cross timbers to the east of our area are of the same formation); (5) river terrace gravel beds, such as those about Austin.

The character of the formation varies with the underground water conditions. Where the porous textured sand or gravel beds lie so that the soil water level is easily available, the formation is a compact forest with a mixture of semi-mesophytic trees filled in by a lower zone of shrubby species. Such is the character of the formation in the Fredericksburg district and in the upper cross timbers. More frequently, however, the soil water conditions are not so favorable, and as a consequence the formation more nearly reflects the normal climatic conditions, as in the granite country. Then it is no longer a compact forest, but an open timbered grass plain where the trees are of low stature and broad spreading crown, each with the individuality of orchard trees. As a consequence of this open formation, such a forest displays no cooperative capacity in producing

a shaded zone, or in collecting humus materials. This leaves a practically continuous grass floor. It also permits the encroachment of sun loving species of the chaparral formations, notably mesquite. Thus many miles of the granite area are covered with a thick growth of mesquite chaparral, with undergrowth of prickly pear and several woody species of the Rio Grande chaparral.

FIG. 15.—*Quercus grisea* and Juniperus formations on an outlying butte of the Staked plains, Big springs; common formation on buttes in western part of central provinces.

The post oak formation of the Rio Grande plain is, as suggested, a southwesterly continuation of the timber of the Fayette prairie sands (in reality of the east Texas forest belt). The southwesterly extension of the formation carries it beyond the Nuéces river, but it has been met by a more vigorous expansion of the Rio Grande chaparral, which has covered the plain as far east as the Guadalupe with a dense mesquite jungle and its accompanying undergrowth of prickly pear.

XEROPHYTIC LIVE OAK FORMATION OF THE OPEN GRASS PLAINS.—That part of Texas lying between the 97th and 100th

meridians, that is the transition from mesophytic to xerophytic zones, is often called the live oak belt because of the characteristic occurrence of *Quercus Virginiana*. The live oak formation of the central erosion area has already been described. This is in reality a part of the live oak belt, but the characteristic occurrence of the live oak throughout its zone is upon the open grass plains of the central region from the Gulf to Red river.

It occurs in so open and irregular a manner as barely to deserve the name of formation. It is in reality a punctuating feature in a pure grass plain formation. The occurrence is in small isolated clumps whose ecology is that during the first years of growth a successful struggle against grazing animals and other encroaching agencies is best waged from these compact masses, which themselves come to have the form of crown and individuality of a single tree. These clumps may be called centers of infection, for by them the species is spreading. Some exceptions to the very open formation occur, as in Live Oak and Bee counties, where the live oak timber becomes a very prominent feature of the landscape.

The species in this zone is very hardy, and attains a great age and large growth. The characteristic growth is expressed in the following dimensions, which though far above the average as to actual size are by no means unusual; diameter of trunk four feet; height of trunk to main branches six to eight feet; total height of tree thirty to forty feet; spread of crown one hundred feet.

MESOPHYTIC FOREST FORMATIONS OF THE STREAMWAYS.—There are two general types of this formation, namely that of the open streamways or broader alluvial river valleys, and that of the enclosed box cañons of the erosion areas.

Timber formations of open streamways.— It happens that, excepting the Rio Grande and Nuéces, the larger rivers rise in regions of very low rainfall, and lead into zones of greater (often heavy) rainfall. It happens, also, that the direction of flow brings them within or accessible to the east Texas forest belt. The result is that the streamways are lines along which

some elements of the forest belt spread into regions far beyond its normal boundaries. Thus, the Red river, Trinity, and Brazos carry purely mesophytic forests to the 97th meridian, and heavy timber far into the central province; and the Colorado, aside from the timber of its cañon course, carries big growths of pecan and sycamore beyond the 101st meridian.

Floristically the streamway formation does not include the

FIG. 16.—Chaparral formation on Staked plains débris, Big springs; a northeastern extension of the trans-Pecos Sonoran chaparral belt.

species which give the east Texas forest its distinctive character. The pines, gums, magnolia, maple, and water oaks are not present, but on the contrary a selected group of species, which more readily adapt themselves to conditions of the open country, greater exposure to dry winds, greater sunlight, and less available water supply. Such are the hackberry, pecan, sycamore, elms, and some oaks. These species are constant associates in the streamway timber of the prairies. Farther out on the plains, toward the headwaters of the rivers, after the streamway timber above described has ended, the plains cottonwood occurs in its characteristic "groves" about basin springs, as, for example, at Big springs, and in similar places in trans-Pecos Texas.

The Nuéces river, notwithstanding its course through the semi-arid Rio Grande plain, and its distance westward from continuous forest areas (below its cañon), is accompanied by a narrow belt of mesophytic timber of which the largest growths are the species just cited for the other streamways. Other species from the southwest, habitually only shrubs, here become small trees.

The timber of the Rio Grande valley presents three types of formation. The first is the cottonwood-willow association above the Grand cañon, with the Texas green ash (*Fraxinus Berlandieriana*), and two or three minor species in the side cañons of the Great bend. In the heavily timbered Cibolo cañon, for example, Havard reported *Populus Fremontii* four to five feet in diameter, and Texas green ash forty to fifty feet high and one to two feet in diameter. The second type, which is mainly that of the river valleys of the Nuéces and other rivers eastward, occupies the middle course of the Rio Grande below Eagle pass, but is at best a very insignificant feature. The third type occupies the valley below Rio Grande city. This is a mixture of eastern river valley species with species of the warmer Mexican region, as *Ehretia elliptica*, *Bumelia lycioides*, and several Mimoseae which have here become fair sized trees. The tropical affinities are finally marked in the lower course of the river by the appearance of an open formation of *Sabal Mexicana*, a tree twenty to thirty feet high.

Timber formations of the box cañons.—Streams which rise in or cut across the central erosion area of the Edwards plateau have worn deep and narrow channels known as box cañons, which in many cases are so sheltered and well-watered as to furnish proper conditions for typical mesophytic vegetation. Such cañons, for example, are those of the Guadalupe system and the Perdenales. The woody vegetation in these cañons, as well as the herbaceous, is that of the interior margin of the Atlantic coast plain, and yet it is to be noted how isolated these cañons are with respect to the mesophytic regions of the coast plain. In the Turtle creek cañon in Kerr county sixteen species of

trees and shrubs were found which are not a part of the typical xerophytic woody vegetation of the region, but are the commonest elements of the Atlantic coast plain forests. Herbaceous species like Ranunculus, Aquilegia, Botrychium, and Dryopteris were naturally associated in this formation. The timber growth

FIG. 17.—A red beds prairie, central province; the spread of mesquite is shown.—From Hill's Phys. Geog. Texas.

attains large dimensions in some of these cañons. On the Guadalupe at Kerrville a cypress stump (*Taxodium distichum*) was found measuring over four feet in diameter.

Mention has already been made of the mesophytic cañon timber of trans-Pecos Texas in connection with high mountain forests and the Rio Grande cottonwood-willow and ash timber. These cañons also furnish shelter for a few semitropical, mostly xerophytic, species common to the lower Rio Grande.

CHAPARRAL FORMATIONS.

The term chaparral as here employed is designed to carry with it not merely the idea of a shrubby formation as opposed to an arborescent one, but also a formation occupying a specific relation to ecological factors. It is a woody vegetation of warm temperate or semi-tropical requirements; adjusted to hydrometeoric conditions wherein there is a minimum of rainfall, a dry air subject to regularly recurring movements of great velocity, and a high percentage of days of intense sunshine; related to edaphic factors in which the soil (waiving its possible great fertility or the fact that it may have had a flood débris origin) has the loose, shifting, uncohesive quality of soils formed by dry weathering and destitute of vegetable mould, if not gravelly or stony: and where the soil water level is too deep to be available for any but perennial plants with far reaching roots. Such conditions of course dwarf the growth of any woody plant subjected to them, even if it could endure them at all. Chaparral is the product of such conditions, and while characteristically shrubby, many species may under other conditions attain to arborescent size, never of course becoming large trees.

There are two general types of chaparral formation in the West Texas region, differing both floristically and ecologically. One is the chaparral of the Rio Grande plain, the other that of the trans-Pecos region. The difference between these two formations is due primarily to the climatic differences between the two provinces, and secondarily to differences in geologic and physiographic conditions.

THE RIO GRANDE CHAPARRAL.— This formation is typically a low, more or less impenetrable bush vegetation, covering continuously vast areas, and varying in height from two or three feet to ten or fifteen, according to varying ecological conditions. In the former case, the habitually shrubby and more xerophytic species prevail, for example within twenty miles of the Rio Grande from Del Rio to Laredo; in the latter, the larger species of Mimoseae form the main body of the formation, notably *Prosopis juliflora* as found from San Antonio to Kenedy. No

fewer than forty species associate in this formation, in many cases a limited area being tolerably uniformly covered by at least half of all the species (*figs. 7–10*). On the other hand, a single species constitutes almost the entire formation over extensive tracts.

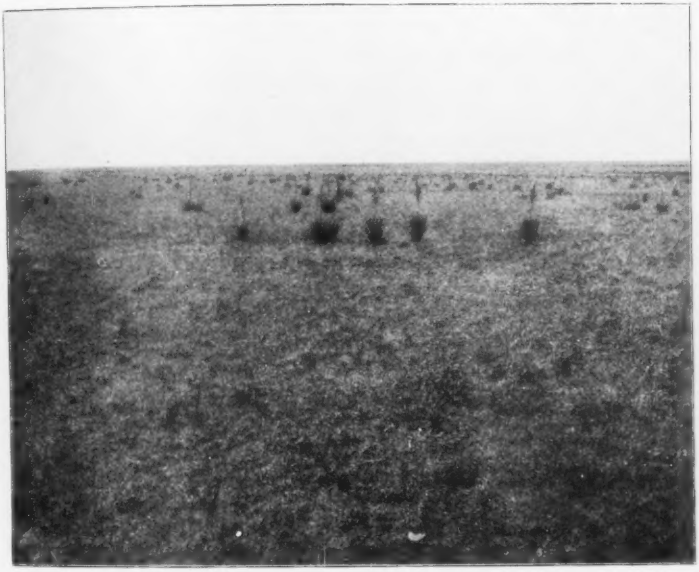

FIG. 18.—Summit of the Staked plains, 3,700 ft. alt.; grass formation with *Yucca glauca*.

On the basis of temperature, there is a distinction of species into those of semitropical and even tropical affinities and those able to endure the freezing winter temperatures of the warm temperate zone. The former occur chiefly in the lower Rio Grande country, the latter constitute the chaparral of the northern half of the plain, spreading also by some species into central Texas. Geological structure and conditions of soil act powerfully to determine the *facies* of the formation upon any given area. Thus, gravelly slopes, denuded of finer sediment, may

have a pure formation of straggling *Parkinsonia Texana*, and basalt ridges are thickly covered by a short bushy formation of *Acacia Berlandieri*. The prevalence of Mimoseae and Caesalpineae in the Rio Grande chaparral deserves special mention. No less than 30 per cent. of the number of species and a far higher percentage of actual individuals would represent the strength of these elements in the formation. This also emphasizes the semitropical affinities of the formation. The condition now prevalent in the Rio Grande province represents a state of unstable equilibrium between chaparral and grass formations (*fig. 8*). These conditions are of a nature to favor the encroachment of the chaparral. This interesting phenomenon is discussed elsewhere in this paper.

Coming next to consider individual features of the chaparral, certain conspicuous types are of special prominence.

Prosopis juliflora or mesquite formation.—In the Rio Grande plain this occupies the level areas of fine compact silty débris. Similar "mesquite flats," as they are commonly called, are found in similar situations throughout the lower Sonoran area in Texas, but the species also occupies black prairie soils in some areas. The most massive formation of mesquite occurs on the silty débris plains on the northeastern border of the Rio Grande plain near San Antonio. From thence southeastward the country is a vast mesquite forest some fifty years old and fifteen to twenty feet tall. In the lower Rio Grande valley individual trees attain (for this species) gigantic size, reaching two feet in diameter and thirty-five feet in height.

Acacia Farnesiana or huisache formation.—This prevails especially on the low moister coast prairie clays. The species is more limited than the mesquite in both moisture and temperature requirements. Its spread has been on the coast prairie as far east as Galveston. Although cultivated as far inland as at Austin, its natural spread is not much beyond the coast country and the lower Rio Grande.

Acacia amentacea formation.—This formation is the prevalent one in the northern half of the Rio Grande province. It is the

"black chaparral," whose foliage and beans yield tons of forage. It constitutes 60 to 75 per cent. of the shrubby vegetation on many thousands of acres in Maverick, Dimmitt, and Webb counties (*fig. 9.*)

Acacia Wrightii formation.—This is known as "bee blossom,"

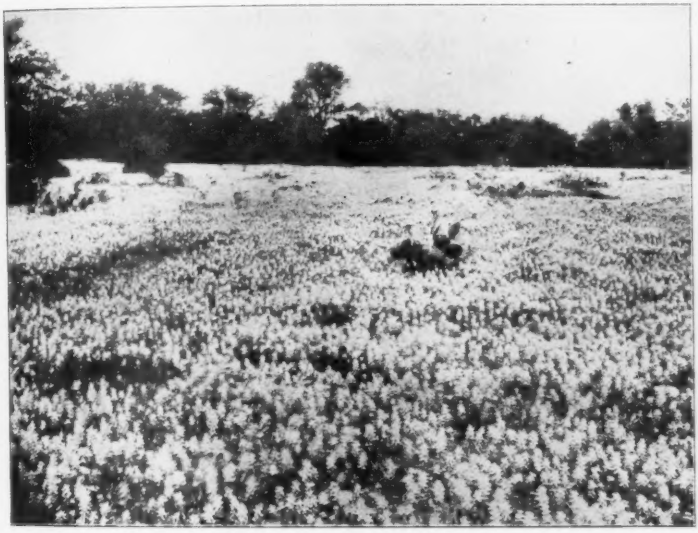

FIG. 19.—Pure formation of *Lupinus subcarnosus* at Austin; a type of prairie annual.

and "cats claw," and is especially prevalent in the northern part of the province between the Nuéces and Medina rivers. Generally it is an open formation on grass plains, and is frequently of low arborescent dimensions.

Acacia Berlandieri or huajillo formation.—This is a very striking vegetation occupying the basalt ridges and cones extending east and west along the northern border of the province. Farther southeast the formation has been noted on coarse gravelly ridges denuded of finer sediment. Everywhere its height scarcely exceeds three or four feet.

Parkinsonia Texana formation.—The coarse gravelly débris slopes in the Eagle pass quarter of the province are occupied by this species. It is an habitually procumbent or straggling and spreading shrub which, while occupying the ground fully, is a very diffuse covering.

Leucophyllum Texanum formation.—This species occurs in solid mass in the more arid parts of the province, especially within twenty miles of the Rio Grande on both the Texan and Mexican sides. The hairy felt covering of the foliage gives it a light tone which is very striking to the eye.

Opuntia Lindheimeri formation.—As an ecological type it is scarcely consistent to class this succulent with dwarf lignescent vegetation, and as such a type it is discussed elsewhere (see under "succulent vegetation"). But the "prickly pear" is so thoroughly a part of the bush vegetation of the Rio Grande country as to necessitate its mention here. The association of this species with mesquite has been remarked. Together they have preempted a vast amount of territory, and have introduced economic problems of no small concern, as well as interesting ecological phenomena.

On the upper course of the Rio Grande, within the Rio Grande plain, the chaparral formation assumes a more xerophytic aspect, and species of the trans-Pecos chaparral appear. A transverse section across the Rio Grande embayment from northeast to southwest would encounter this same transition to the extreme xerophytic type on the Mexican side, where the central plateau and sierra region begins, that is, at the outer rim of the embayment.

THE TRANS-PECOS CHAPARRAL.—The area covered by this type of chaparral embraces, besides trans-Pecos Texas, the north Mexican plateau and the arid lower Sonoran zone plateaus of New Mexico, Arizona, and southern California. Its northeastern extension includes the western part of the Edwards plateau and the southern slope of the Staked plains.

In the trans-Pecos region the formation occupies the cañon sides and bluffs from the Pecos westward, the rougher southern

end of the Stockton plateau, the lower slopes and foothills, the arid mountain slopes (especially in the Great bend), the dry cañons of the Great bend region, and the bolson deserts. On the whole it is more of a rock vegetation than the Rio Grande chaparral, but it also occupies the finer débris-covered slopes and bolson plains.

Compared with the Rio Grande chaparral it is in large measure floristically different. Where it contains the same species, as for example *Prosopis juliflora*, the habit is very different, being in this case dwarfed and shrubby bushes, while in the Rio Grande plain it is habitually low arborescent. The Mimoseae and Caesalpineae form less than 10 per cent. of the species, individuals occur less abundantly, and, excepting *Prosopis juliflora*, are different species from those of the Rio Grande plain. A more striking individuality as ecological types is attained in the species of this formation. This is seen in the greater abundance of the Ephedra type, the felt-covered Eurotia and Croton type, those impregnated with volatile resins, like Larrea and Flourensia, and the wand-like, fluted, thorny stems of Fouquiera (*fig. 20*).

About thirty species are recognized as more or less prominent constituents of chaparral formation of the trans-Pecos Texas. Apparently not so great a percentage of these species associate on any one area to constitute the formation, though the number of species occurring, for example, on the sides and bluff of the Pecos cañon would be little less than half the total. Considering types of the trans-Pecos chaparral formation in detail, it must suffice to point out the following.

Larrea Mexicana or Mexican greasewood formation.—This is by far the most notable formation of any single species. It is especially characteristic of high gravelly mesas (as about Fort Bliss, El Paso), and of the bolson deserts, extending even to highly charged alkaline soils at the center of such basins (*fig. 21*). This greasewood formation is composed of such regular open growth as to appear like plantations. The plant is a shrub with spreading top, averaging less than three feet tall. Its special

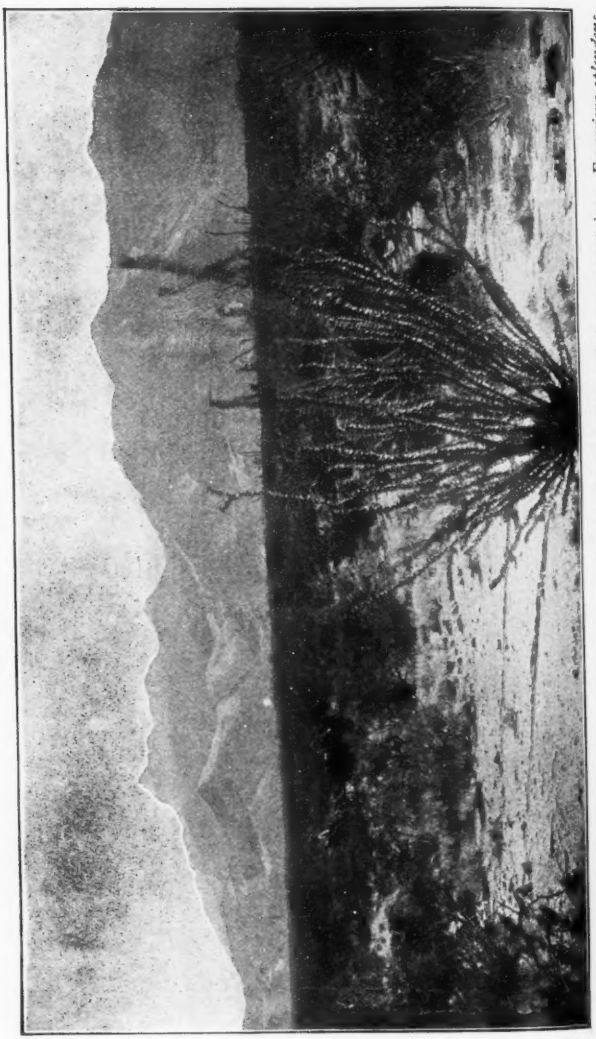

FIG. 20.—Chaparral formation on desert basin southwest of Sierra Blanca Quitman mountains; *Fouquiera splendens* in the foreground.—From Hill's Phys. Geog. Texas.

adaptation seems to lie in the great quantity of resinous matter in the leaves. The odor from this gives notice of the nearness of a greasewood formation.

THE TRANS-PECOS TYPE OF CHAPARRAL EAST OF THE PECOS.—As already noted, this chaparral spreads east of the Pecos upon the western margin of the Edwards plateau, especially its plains area, and upon the southern border of the Staked plains. The easterly extension of the more arid lower Sonoran area is indicated in this chaparral. A typical case may be cited in the vicinity of Big springs in Howard county (*fig. 16*). This is a region covered by the plains débris. The arid mesas are covered by a characteristic formation of chaparral in which not less than twenty species occur, among which are more than 50 per cent. of the characteristic trans-Pecos species.

THE RIO GRANDE CHAPARRAL IN CENTRAL TEXAS.—The chaparral of the Rio Grande plain terminates abruptly at the foot of the Balcones escarpment, where the xerophytic forest of the erosion area begins. A few species, however, mingle with the timber species, and occasionally (as in the case of *Condalia obovata*, *Zizyphus obtusifolia*, and others) forms a characteristic chaparral bush or thicket. On the grass plains of the granite country a much more pronounced encroachment of woody vegetation is taking place. As already pointed out, the mesquite has spread over most of the province. With it have gone the prickly pear and several shrubby species which together are building up a compact chaparral formation. The Rio Grande Mimoseae, except Prosopis, and Caesalpineae, and all others of the more characteristic species, do not appear in this chaparral.

FORMATIONS OF SUCCULENT OR WATER-STORAGE VEGETATION.

This third general type of formation stands out in strong contrast with the two preceding types of grass and woody vegetation. The contrast lies in the fact that whereas the preceding types have adjusted themselves to xerophytic conditions by retaining the least amount of sap-bearing tissue, this type has gone exactly to the opposite extreme. The areas occupied by

formations of this type are also in the main different from those of the other two. With few exceptions, this latter might be designated as a kind of rock vegetation, for the most significant elements are constantly associated with high, arid, stony slopes. As an ecological type the succulent vegetation is to be regarded as a more efficient adaptation to extreme aridity than the grass or woody vegetation. Consequently, it is to be found in its most typical display in the arid regions of trans-Pecos Texas.

In this discussion little account can be taken of the numerous ephemeral species like those of Sedum, Talinum, Portulaca, and others, but the consideration is particularly given to those more evident as features in the landscape. Of the elements composing this more conspicuous vegetation, there are three types, each forming a distinct and close genetic group. These are the Cactaceae, the Yucceae, and the Agaveae. A brief consideration of these may precede the discussion of the three types as associated in a single formation.

THE CACTUS VEGETATION.

A rather general survey of this group gives three types, each associated with a distinct physiographic feature: (1) the flat-jointed opuntias of the Rio Grande plain and central Texas; (2) the woody cylindrical-stemmed opuntias of the high plateau plains; and (3) the cylindrical and spherical cacti of arid stony slopes.

Opuntia Lindheimeri formation.—The prevalence of this formation in the Rio Grande plain has already been noted in discussing chaparral vegetation. The species here considered has spread beyond the Rio Grande plain to the north and east beyond the Colorado. To the east and southeast of Austin there are some extensive and typical prickly pear fields. It is present with the mesquite in the granite country in great abundance. In the Rio Grande plain the quantity of vegetation formed by this species is of almost incredible bulk. The level silty débris plains are its common habitat, but stunted formations of it also occur on arid gravelly soils, and on chalk soils

about Austin. In the valley of the Nuéces river, about midway of the plain, this Opuntia attains gigantic size, being said to exceed a height of ten feet. In the vast mesquite forest on the northeastern border of the Rio Grande country, the prickly pear is an undergowth four or five feet high. These two species together are practically blocking up large tracts of pasture lands, not only changing grazing conditions, but rendering the use of such lands for agricultural purposes an expensive enterprise.

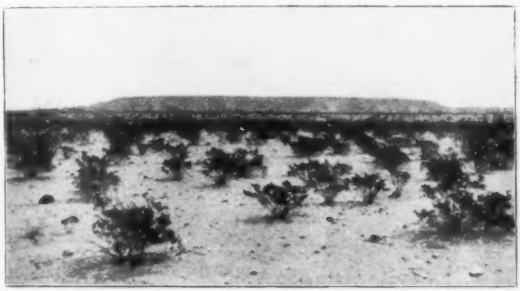

FIG. 21.—*Larrea Mexicana* (Mexican greasewood) formation; typical bolson desert of trans-Pecos Texas; *Fouquiera splendens* associated here.—Kodak view by R. T. Hill.

This Opuntia fruits regularly and in great quantity, and apparently is chiefly spread by means of seeds. These have been found germinating in great numbers in cow chips. The juicy fruits are eaten not only by cattle, but evidently by other mammals as well, and by birds.

THE CYLINDRICAL OPUNTIAS.—These are chiefly plants of the high plains westward, *Opuntia frutescens* being an exception. This species is part of the chaparral of the Rio Grande plain and the adjacent provinces northward. It occurs especially in association with spreading shrubby species by which it partially supports its slender stems, and together forming well-defended clumps of chaparral, from which there is a gradual encroachment upon the grass formation. The presence of the Opuntia prevents the shrubs from being eaten back by cattle. *Opuntia arborescens*

is conspicuous on the high grass plains of the Stockton plateau and westward. It also occurs east of the Pecos at the foot of the Staked plains, and to a less degree on the summit of the south half of the plains. At the base of the plains in Borden county it is very common and of large size, reaching seven and eight feet in height. This Opuntia does not occur as a continuous formation, but at intervals serving rather to punctuate the grassy landscape. This is always noted by travelers who observe the landscape of the trans-Pecos grass plains traversed by the railways.

THE BROAD CYLINDRICAL AND SPHERICAL CACTI occur upon arid stony slopes of trans-Pecos Texas as the most extreme type. These associate with Agaveae and Yucceae to make the type of formation to be discussed subsequently. East of the Pecos, on stony hillsides, rock bluffs, and even on coarser gravel ridges, cespitose species of Cereus occur, often (as in the case of *C. caespitosus*) forming patches from a few yards to many rods in diameter, as on broken granite slopes in Llano county.

THE YUCCA VEGETATION.

The prominent yucca vegetation of the so-called "yucca belts" is a part of a mixed formation to be considered presently. Independently of this, certain areas of yucca vegetation are to be noted (*fig. 24*). First, the occurrence of *Yucca Treculeana* in the lower Rio Grande and Gulf coast region, where it is said to form "open stunted forests." Again on the cañon sides in the central erosion area the same species (apparently) forms a conspicuous feature of the cañon flora. Second, the constant occurrence of *Yucca rupicola* upon the talus débris of slopes leading down from crumbling limestone formations. The formation, of which this is but an element, is one of the most distinct minor formations of the cretaceous areas east of the Pecos. Third, *Yucca angustifolia* is particularly characteristic of the Staked plains region. Here it follows the gentle slopes about shallow basins or the wave-like undulations where the soil is looser and more sandy. Fourth, Nolina formations on the Rio Grande

plain below the Balcones escarpment, and at many places on stony slopes as far east as the Colorado. The great tufts of this so-called bunch grass form the most conspicuous vegetation on the finer débris below the yucca belt in the Rio Grande plain.

THE AGAVE VEGETATION.

In addition to species of the Agaveae which associate in the mixed cactus-yucca-agave formation to be next described, two species require notice. *Agave Wislizeni*, or "Texas mescal," is a mountain species (apparently upper Sonoran to Transition) occurring (according to Dr. Havard) in all the mountains of western Texas, and formerly much used for food, beverage, and medicine. *Agave Americana*, or "Mexican maguey," enters the Texas region in the lower Rio Grande plain, and two or three more insignificant species are also present.

MIXED CACTUS, YUCCA, AND AGAVE FORMATION OF ARID STONY SLOPES.

While the trans-Pecos region possesses more or less of each of the three types included in the above named formation, in most of its physiographic provinces a little investigation shows that in the main the three are found upon one type of physiographic structure, either more or less equally represented, or one type predominating. In traversing the high grass plains of the Stockton plateau and westward it is noticed that in approaching the crest of one of the broad undulations, or any relief feature notably above the plains level, a unique yucca vegetation sets in, to be followed again presently by other stretches of grass plain. Where the margin of the plain rises up into the bordering foothills, there again is the yucca vegetation. Again, on the rim of the enclosed bolson basins this formation is present, and finally on many of the gentler slopes of the mountains (especially those with timberless arid slopes) the yucca vegetation is present as the chief vegetation feature. This is the apparent condition seen at a distance, and sometimes the Yucceae are alone in the formation. But a nearer look commonly reveals the less conspicuous cactus and agave members of the association (*fig. 22*). In all the physiographic features cited, practically the same

FIG. 23.—Vinton spare-rocky formation of stony slopes; mountains of the Great bend of the Rio Grande, in trans-Pecos Texas. Photograph by Shear, 1901.

ecological conditions prevail. In the wearing away of the mountains in this dry climate the débris is carried downward to fill the intervening basins. The finer débris being carried nearest the basin center, on the slopes at the outer rim of the basin lies the coarser débris, an unconformable mass of coarser or finer stony talus. This talus débris may extend far up the slopes of mountains, which receive but a few inches of rainfall annually, especially those in the Great bend, and thus carry the formation of cactus, yucca, and agave with it. These "yucca belts," as Mr. Hill calls them, when projected upon a map appear as marginal lines of basins and to encircle the various mass elevations. The formation extends even to the east of the Pecos cañon along the coarse débris from the Balcones escarpment. The abundant occurrence of *Yucca Treculeana* and several species of cacti on the timberless cañon sides as far east as the Colorado may be regarded as an extension of the same formation.

As to the prominence of the several types in the formation, as already stated, viewed from a distance the yucca vegetation seems the only prominent one. It is in reality so only in some instances. In other cases other types play the chief rôle, so that several variations exist, as illustrated by the following:

Open forest-like formations of the palmo or Yucca macrocarpa.—This largest of our yuccas is very abundant in the Great bend region, covering the long arid slopes with an open formation of yucca trees "with caudex ten to twenty feet high and one to two feet in diameter" (Havard).

Lechuguilla (*Agave heteracantha*) *and sotol* (*Dasylirion Texanum*) *formation.*—This is a very characteristic formation of very rough stony slopes in which the lechuguilla forms a most obnoxious feature because of its agressive short bayonet-like leaves. This formation is very common as far east as the Nuéces cañon.

Formations in which globular and cylindrical cacti predominate.—These include several species of Mamillaria (among them forms called "devils pin cushion"), Cereus (notably the strawberry cactus, *C. stramineus*), Echinocactus (especially the "Turk's head," *E. longihamatus*), and Anhalonium. Such formations

indicate about the ultimate point of extreme exposure to intense light, burning midday and chilling midnight temperatures, and moistureless air and soil.

There is still another and very striking species associated with the cactus-yucca-agave formation, especially on the most arid stony mesas and slopes where cacti predominate. This is *Fouquiera splendens*. Its slender, thorny, wand-like stems arise in small groups from the surface of the ground to the height of five to eight feet, bearing leaves only in a tuft at the apex. It is as if the most arid spots had been located and marked out by this plant (*fig. 20*).

ROCK VEGETATION OF CRYPTOGAMOUS PLANTS.

The formation of succulent vegetation might be designated, on the whole, rock vegetation, occurring as it does either upon stony talus or on cañon bluffs. Certainly many succulents not mentioned in the discussion are characteristic rock plants, but the attempt here is to select types of formation which in a peculiar or conspicuous way constitute the characteristic vegetation. The xerophytic cryptogamous plants constitute such a vegetation. They are a rock vegetation either because they occur upon a bare rock substratum or because they inhabit clefts or fissures in the rocks, or dry rock ledges. The former play an important rôle in disintegrating solid rock, as the granitic lichens, or in promoting the accumulation of a matrix of organic material upon barren surfaces, as the Cyanophyceae on bare chalk or compact limestone débris. Throughout the central Texas Cretaceous areas the occurrence of these low plants is very noteworthy. They consist of a species of Nostoc which occurs in curled, crumpled masses after rains or foggy weather, literally covering the ground; a mat-forming Scytonema; and several matted, leathery lichens.

The so-called rock ferns are ecologically the most noteworthy elements of the vegetation of rock fissures and ledges. The several genera and numerous species of ferns constituting this xerophytic group are associated with the Sonoran climatic

FIG. 23.—A dead "bunch-grass" desert, adobe soil; Tomillo desert, trans-Pecos Texas.—Photograph by R. T. Hill.

conditions of the southwest, and occur not only throughout that area, but over its southward extension along the continental axis south of the equator. Their distribution in the west Texas region coincides with the areas of escarpment, and of cañon erosion. They occur, for example, throughout the central erosion area. Aside from the various means of adapting the vegetative plant to xerophytic conditions, the ecological relations of this group of ferns has not been much studied.

Two additional important species are to be noted, namely, *Selaginella lepidophylla* (a "resurrection" plant) of the trans-Pecos region, but also extending eastward on limestone bluffs and knobs to the Frio river; and *Selaginella rupestris* (the forms still so designated) is especially abundant in the granite area, but it appears to be in all of the mountainous or hilly areas of west Texas (on dry gravel ridges at Austin), on limestone hills on the upper Nuéces cañon, and in trans-Pecos mountains. Several extremely xerophytic mosses are essentially rock plants. Some form close velvety masses on granite and sandstone. Other species occur with *Selaginella rupestris*, and Scytonema, and lichen mats on the dry gravel ridges and on compact limestone débris. Several xerophytic species of liverworts occur upon granite fissures and upon gravelly soils, notably three or four species of Ricciaceae.

HALOPHYTIC VEGETATION.

The areas in the west Texas region in which the soil is impregnated with alkali sufficient to affect the vegetation covering are rather large and widely distributed, and have been but little investigated from a botanical point of view. There are included here in general (1) the gulf coast, (2) basins in the lower Rio Grande plain, (3) the gypsum beds of the red beds country, (4) the alkali basins of the western side of the Staked plains, (5) the Pecos valley or Toyah basin, (6) the bolson basins of trans-Pecos Texas of which the Howard and Hueco bolsons are the largest.

From Dr. Havard's description of the "Pecos flats" and of

Salt lake basin (the Howard basin), it appears that the two types of vegetation on these alkaline flats are grass and chaparral formations. He says (*loc. cit.*, p. 465) "the prevalent grass of the Pecos flats and often the only kind is *Sporobolus airoides*, with erect culm one to three feet high, and loose open panicle. It is distinctly salt to the taste," etc. "On alkaline soils occur the fleshy chenopods *Suaeda suffruticosa* and *S. depressa*, and *Spirostachys occidentalis*." Of the Howard basin he says (p. 497) "the smooth, broad beach of the lakes (occupying the center of this basin) more or less incrusted with alkali is absolutely bare. Here and there low sand hillocks are covered with *Spirostachys occidentalis*, *Larrea Mexicana*, and *Frankenia Jamesii*." The salt grasses of the northern extremity of the basin consist mostly of *Sporobolus airoides* and *S. Wrightii*.

Detailed information of the vegetation of alkaline basins or of the Gulf coast within the region here considered is not sufficient to warrant further discussion.

CHANGES IN PREVALENT FORMATIONS DUE TO AGENCIES OF CIVILIZATION OR OTHER CAUSES.

The equilibrium established upon the vegetation of the west Texas region as a resultant of all the forces playing upon it has been destroyed by the introduction of new forces chiefly due to human agency. As a consequence, the vegetation of the region is undergoing some profound changes. Under the reign of equilibrium the trend was decidedly toward the establishment of solid grass formations, thus making the region one of open grass prairies and plains. The present trend is decidedly toward the establishment of woody vegetation, either shrubby or dwarfed arborescent, with a coincident driving out of sun-loving species (especially grasses) and favoring of the shade-loving ones.

Other changes not in the direction of establishing a woody vegetation are taking place. For example, in the constitution of the grass formations Jared G. Smith observes (Bull. 16, U. S. Div. Agrost., p. 28) "before the ranges were overgrazed, the grasses of the red prairies were largely blue stems or sage

FIG. 34.—Yucca formation on foothills of Chisos mountains, trans-Pecos Texas; Yucca ("palmella") and sotol (*Dasylirion Texanum*); oak in the background probably *Q. Emoryi*.

grasses (Andropogon), often as high as a horse's back. After pasturing and subsequent trampling and hardening of the soil the dog grasses or needle grasses took the whole country. After further overstocking and trampling the needle grasses were driven out and the mesquite grasses (Hilaria and Bulbilis) became the most prominent species."

There is a further strong tendency toward the establishment of a weed vegetation to the disadvantage of what may be called the native vegetation. Such for example are *Gutierrezia Texana* and *Croton Texensis*.

Regarding the establishment of woody vegetation, it is the unanimous testimony of men of long observation that most of the chaparral and mesquite covered country was formerly open grass prairie. This applied to the Rio Grande plain, as well as to the mesquite flats of the central provinces. Illustrations are everywhere at hand. At Austin, for example, many black land pastures have within a few years become covered by a perfect jungle of mesquite.

Apparently under the open prairie régime the equilibrium was maintained by more or less regular recurrence of prairie fires. This, of course, is by no means a new idea, but the strength of it lies in the fact that the grass vegetation was tolerant of fires and the woody vegetation was not. It was only after weakening the grass floor by heavy pasturing and ceasing to ward off the encroaching species by fire that the latter invaded the grass lands. Once the equilibrium was destroyed everything conspired to hasten the encroachment of chaparral—droughts, pasturing, trampling, seed scattering, and so on. As Smith pointed out, a mesquite tree once established became a center of infection in offering shelter for shrubby plants and shade-loving grasses, driving out the native prairie grasses. In brief, the efforts to exploit the wealth of grass lands for profit, namely stock raising, have been the main agency in transforming them rapidly into lands covered by a totally different and far less valuable vegetation.

Another economic question arises from artificial change of

plant formations, though exactly the reverse of the preceding discussion, namely, in destroying the woody vegetation of certain areas. The great demand for charcoal, fuel, posts, and rough construction timber, and the desire to secure small patches for temporary cultivation are resulting in a rapid removal of the xerophytic timber vegetation and the cañon timber from the hill country of the Edward's plateau. This brings up the question of the relation of this timber vegetation to the water supply, to soil erosion, and to destructive floods. In some cases, at least, this formation is succeeded by the rock vegetation and the adobe vegetation of the Cretaceous areas, which establish themselves as a result of denudation by erosion which follows removal of the timber covering.

SUMMARY.

1. By reason of its geographic extent and position and of its relief, the west Texas region possesses floral elements ranging in their temperature relation from tropical to transition.

2. In its climatic relations the region falls partly under the eastern or Atlantic type (Gulf type, Great plains type), and partly under the Pacific (Yuma type, Mexican type). This brings about great diversity of vegetation in the moisture relation.

3. This region is the meeting ground of the following floral elements: (1) the Gulf neotropical; (2) the Mexican semitropical; (3) the Austro-riparian and Carolinian; (4) the Great plains upper Sonoran; (5) the north central prairie region; (6) the Rocky mountain; (7) the south plateau (of the Rocky mountains) upper Sonoran; (8) the arid plateau and bolson desert lower Sonoran.

4. The physiographic and geologic provinces coincide in general with vegetation provinces distinguished by characteristic vegetation formations.

5. The flora of the entire region is one of xerophytic aspect, but of several grades from semi-arid to extremely arid. Broad streamways and cañons and high mountains carry mesophytic vegetation into the heart of the region.

6. Annuals whose vegetation period covers only a few weeks exist generally in pure formation in all parts of the region having a constant annual recurrence of temperature and moisture conditions suited to the species in question. Thus the plains from the lower Rio Grande to the Red river and northward may possess successively the same ephemeral but extremely brilliant formations.

7. The vegetation native to the region before the coming of civilization is undergoing profound changes as a result of disturbed equilibrium. This is no doubt exterminating certain species, epecially grasses. The chief results of the changes appear in establishing a woody or weed vegetation, and in the denudation of the hill country.

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FURTHER NOTES ON THE PHYSIOLOGY OF POLYMORPHISM IN GREEN ALGAE.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXXII.

BURTON EDWARD LIVINGSTON.

SINCE the publication of the previous article on this subject[1] several additional lines of experimentation have been completed. The results of these will be given in the present paper. They corroborate the conclusions already expressed, and also throw some further light upon the interesting response with which we are dealing.

I. PHYSIOLOGICAL EXPERIMENTS.

The experiments here recorded were all performed upon the organism used in the previous work, that is, *Stigeoclonium tenue* (?), and the same methods were employed as far as the culture media would allow. The cultures may be classified according to the media used into the following groups: (1) sugar solutions, (2) solutions containing both sugar and mineral salts, (3) porous plate cultures, (4) gelatine cultures, (5) cultures in darkness, (6) evaporation cultures. These categories will be considered in order.

1. SUGAR SOLUTIONS.

The work already published shows clearly that for changes in concentration of Knop's solution the factor controlling the response of the alga is the osmotic pressure. Whether this acts upon the organism merely through a change in the relation of water to the cell, or in some more complex way, could not be decided as long as the pressure was always produced by mineral salts. Thus the next step to be taken was to determine the effect upon the plant of a solution of non-electrolytes. To this end some

[1] LIVINGSTON, B. E.: On the nature of the stimulus which causes the change of form in polymorphic green algae. BOT. GAZ. **30**: 289. 1900.

substance had to be chosen in which the plant would live and grow for some length of time. Also it was necessary that the culture media be of such nature as not to be readily attacked by bacteria and fungi. After several failures, the two saccharoses, lactose and cane sugar, were hit upon for this purpose. The former is far the better, but the latter serves very well. Cultures in these may be continued for two, three, or even four weeks without undergoing fermentation sufficient to affect the alga appreciably.

Tables I and II give the results of some representative cultures in these solutions. At the left are those in lactose, at the right those in cane sugar. In the first table the original material was of the palmella form; in the second, of the filamentous. The concentrations are given in terms of a normal solution ($n = 1$ gram molecule per liter), and are placed in the columns headed "concentration." In the columns headed "first response," Sp. F. denotes that zoospores were produced in great numbers, and germinated as usual to form filaments. A single asterisk (Sp.*) shows that the spores did not germinate. Filaments produced from the original masses are denoted by *F* in this column. Two asterisks (Sp.**) show that few zoospores were produced, and that these failed to germinate. *P* denotes the palmelloid form; *P*> the rounding up of cells as if going over into palmella. In the columns following those indicating the response is given the time of response in days; 2–12 denotes that the response was observed two days after the making of the culture, and continued for ten days. The second response is the result of evaporation, and comes after a somewhat longer time than the first. The time for it is given in days after the making of the culture.

In general, solutions of low osmotic pressure produce zoospores and filaments, while those of high pressure produce only the round-celled form. This is in accord with the results obtained with solutions of mineral salts. However there is one difference in the behavior of the palmella form in solutions of electrolytes and non-electrolytes. This is brought out by Table

TABLE I.

PALMELLA IN SUGAR SOLUTIONS.

Lactose					Cane Sugar				
Concentration	1st Response	Time	2d Response	Time	Concentration	1st Response	Time	2d Response	Time
$\frac{n}{100}$	Sp. F.	2–12	P	30	$\frac{n}{100}$	Sp. F.	5–10	..	..
$\frac{n}{100}$	Sp. F.	2–7	..	..	$\frac{n}{100}$	Sp. F.	2–9	..	..
$\frac{n}{10}$	Sp. F.	4–9	P	30	$\frac{n}{10}$	Sp. F.	3	..	..
$\frac{n}{10}$	Sp. F.	9	..	..	$\frac{n}{10}$	Sp. F.	2–18	..	..
$\frac{2n}{10}$	Sp. F.	2–12	..	..	$\frac{2n}{10}$	Sp. F.	2–18	..	..
$\frac{3n}{10}$	Sp.* F.	2–7	P	9	$\frac{3n}{10}$	Sp. F.	2–18	P	30
$\frac{4n}{10}$	Sp.** F.	2	P	14	$\frac{4n}{10}$	Sp. F.	8–14	..	..
$\frac{5n}{10}$	No spores P	14	..	..	$\frac{5n}{10}$	Sp.* F.	8	P	14
$\frac{7n}{10}$	P	10	..	..	$\frac{7n}{10}$	P	10	..	..

TABLE II.

FILAMENTS IN SUGAR SOLUTIONS.

Lactose			Cane Sugar		
Concentration	Response	Time	Concentration	Response	Time
..	..	..	$\frac{n}{100}$	Sp. F.	6–13
..	..	..	$\frac{n}{10}$	No spores F	6
..	..	..	$\frac{n}{10}$	Sp.* F P>	4–11
$\frac{3n}{10}$	No spores P>	10	$\frac{3n}{10}$	No spores P>	14
$\frac{5n}{10}$	P	14	$\frac{5n}{10}$	P	8–14
$\frac{5n}{10}$	P	10	$\frac{5n}{10}$	P	10–12
$\frac{7n}{10}$	P	10	$\frac{7n}{10}$	P	10
..	..	..	$\frac{75n}{100}$	P	9

III, which shows the maximum limit for zoospore production in each case. It is to be compared with Table V of the former article,[2] from which the figures for mineral solutions have been taken. The figures have been altered to round numbers to avoid confusion.

TABLE III.

MAXIMUM LIMITS FOR ZOOSPORE PRODUCTION.

Original Form	Mineral Solutions	Solutions of Non-electrolytes	
		Lactose	Cane Sugar
Palmella	$\frac{2n}{10}$	$\frac{5n}{10}$	$\frac{6n}{10}$ — $\frac{7n}{10}$
Filamentous	$\frac{3n}{10}$	$\frac{3n}{10}$	$\frac{3n}{10}$

The filamentous form responds in exactly the same manner whether the solution is of electrolyte or non-electrolyte. But to bring about an inhibition of zoospore production in the palmella form requires a much higher osmotic pressure when this is produced by non-electrolytes than in the other case. Also the two sugars used differ in that the limit for cane sugar is much higher than for lactose. Why is this? The volume of the cells in the culture is so small, as compared with that of the surrounding fluid, that the difference just spoken of cannot be explained by the supposition that the carbohydrate is absorbed and thus the concentration of the medium lowered. The amount of absorption possible would be entirely inadequate to alter the concentration to any appreciable degree. It seems more probable that by absorption of sugar the concentration of the cell sap is increased, thus decreasing the difference between the osmotic conditions within and without the plant, and so weakening the stimulus. This would occur if the carbohydrate molecules were to penetrate the cells (*i. e.*, be absorbed) more rapidly than the ions of an electrolyte. It is possible that cane sugar is absorbed

[2] *Loc cit.*, p. 313.

much more readily than lactose; hence might arise the difference between the effect of these two substances upon the organism.

Considering these results, together with those heretofore published, there seems little room for doubt that the response of this plant is brought about by a change in its relation to water. An increase in the osmotic pressure of the surrounding fluid must invariably extract water from the cell (since plant membranes are readily permeable to water), and a decrease of such pressure must cause the cell to take up more. However, an increase in the amount of sugar in the medium might influence the plant otherwise than in the way just mentioned. There might be, for instance, a chemical effect produced by the carbohydrate molecules. Also, it is readily conceivable that an increase in the number of electrically charged ions in the medium might exert some specific influence upon the protoplasm aside from mere change of water relation. But it is hardly conceivable that any chemical influence exerted by sugar molecules could be identical in its effect with an influence exerted by electrolyte ions. Thus we are almost driven to the following conclusions: (1) since solutions of electrolytes and non-electrolytes affect the organism in the same way, they must exert a common influence upon the cells; and (2) since it is inconceivable that there is any chemical influence common to the two forms of solution, the response must be due to the *one factor which is common to both*, namely, change in the water relation. Whether this change in the water content of the cells acts merely through the mechanical effects of a change in the turgor pressure of the cell sap, or whether the response is brought about by a more subtle adjustment within the protoplasm itself, we have at present no means of telling. It seems probable that both these factors are operative.

It is of interest to note here that while the organism often dies in a mineral solution whose pressure is $\frac{4M}{10}$, and invariably dies in stronger mineral solutions, yet it lives indefinitely and apparently without injury in a normal sugar solution. This is

probably due to the poisonous action of some of the electrolyte ions used. To determine, if possible, what this action may be, will be the object of further research.

The same culture may be made to change its form several times in sugar solutions just as in mineral solutions, by adding water or allowing it to evaporate. Nearly all the cultures made in sugar solutions have been controlled by others made at the same time in mineral solutions, and the control cultures have not deviated at all from those discussed in my previous paper. Further, healthy material taken from sugar solutions behaves in water and in mineral solutions precisely as though it had been grown in a mineral solution.

2. MIXED SOLUTIONS.

These solutions contained both sugar and mineral salts. The response of the alga to the weaker ones is the same as though they were composed either of sugar alone or of salts alone. For the stronger solutions the same is true of the filamentous form. But the palmella form gives something of its characteristic response to sugar or electrolytes, according as one or the other of these substances predominates. However, this was not very well marked in the experiments. In general, the plant behaves in the same manner in a mixed solution as in a simple one.

2. POROUS PLATE CULTURES.

These were made on unglazed porcelain, such as is used in chemical work. A piece of plate four or five centimeters square was laid on the bottom of the culture dish, and sufficient solution was poured over to stand within a millimeter or two of the upper surface of the plate. Thus the plate was saturated, but no free liquid was upon its surface. The alga cells were placed upon the plate and the whole was covered as usual. The results of these cultures are perfectly uniform, and are exactly what would have been expected. The osmotic pressure of the solution which saturates the plate determines the response of the plant. Typical results from the series of plate cultures are presented in table IV. The abbreviations are those used in tables

I and II. Ev denotes an uncovered culture with rapid evaporation.

TABLE IV.

POROUS PLATE CULTURES.

Solution.	Original form.	Response.	Time.	Solution.	Original form.	Response.	Time.
$\frac{n}{100}$ L	P	Sp. F.	9	$\frac{3n}{10}$ K	P	P.	10
$\frac{n}{100}$ S	P	Sp. F.	9	$\frac{4n}{10}$ S	P	Sp. F.	9
$\frac{n}{100}$ K	F	Sp. F.	10	$\frac{4n}{10}$ K	P	P. F.	16
$\frac{n}{10}$ K	F	P. F.	10	$\frac{5n}{10}$ L	P	P.	16
$\frac{2n}{10}$ L	P	Sp. F.	9	$\frac{75n}{100}$ L	P	P.	46
$\frac{3n}{10}$ K	F	P. F.	10	$\frac{n}{100}$ L, Ev	F	P.	6

4. GELATINE CULTURES.

These were made like the plate cultures just described, excepting that in the place of the porcelain support the solution to be used was thickened with gelatin until it would give a firm surface on which to place the alga. The result was uniform with the foregoing. The gelatin itself has no influence. The osmotic pressure of the solution determines the response of the organism. Gelatin cultures cannot be continued very long because of bacterial action, and are therefore not very satisfactory.

5. CULTURES IN DARKNESS.

In darkness the alga remains green and healthy for three to five weeks. At last the cells become plasmolyzed and go to pieces. Putting the culture in darkness has no effect whatever upon the response of the plant. This probably indicates that the mechanism of polymorphism is not connected with that of photosynthesis.

6. EVAPORATION CULTURES.

Weak solutions, with their contained filaments, may be left open to the air, and within a few days become very much concentrated through evaporation. The response of the plant is

rapid and marked in these cases. If one has filaments and wishes the palmelloid form, he has but to leave the dish uncovered for a few days to attain this end. Evaporation affects the plant in the same way whether it be in the case of sugar solution, mineral solution, or porous plate culture. It was impracticable to get results by evaporation from gelatin on account of bacteria, by the growth of which the culture was destroyed before a response could be expected.

SUMMARY.

1. Non-electrolyte solutions have the same effect as electrolyte solutions; the osmotic pressure is the controlling factor in determining the form of the plant. This is effective through changes in the water content of the cells.

2. The threshold of stimulation for inhibition of zoospore production is at a higher concentration in a solution of non-electrolytes than in one of electrolytes. Also, the plant withstands the killing effect of the solution at a higher concentration for non-electrolytes than for electrolytes.

3. This threshold of stimulation for the palmella form is at a higher concentration for cane sugar than for lactose.

4. Cells supported upon gelatin or porcelain plates moistened by a solution respond in the same way as though they were immersed in the solution.

5. Prolonged darkness has no effect upon the form of the plant; the response of polymorphism does not depend upon the photosynthetic process.

6. Increase in concentration caused by evaporation from any solution or from porcelain plates brings about the normal response for a concentrated solution.

II. PHYSICO-CHEMICAL TESTS.

In order to determine the extent of the error introduced into these experiments by the author's assumption[3] of complete ionization in the mineral solutions, a series of tests of the actual

[3] *Loc. cit.*, p. 297.

osmotic pressures developed therein has been carried out during the past summer.

Owing to the as yet insurmountable difficulties in determining directly the osmotic pressure of a solution, the indirect method by freezing points was resorted to. It has been well established[4] that for dilute solutions a uniform relation obtains between the osmotic pressure, the depression of the freezing point, and the elevation of the boiling point. Thus if Δ_f denotes the depression of the freezing point, the osmotic pressure is given by the formula $P_f = 12.07\,\Delta_f$, wherein P_f is the osmotic pressure at the freezing point of the solution. Similarly, $P_b = 57\,\Delta_b$, wherein P_b is the osmotic pressure at the boiling point and Δ_b the elevation of the boiling point. The depression of the freezing point was determined by means of Beckmann's apparatus,[5] for the mineral solutions described in the previous paper, as far as these were at hand when the tests were made. From these data the osmotic pressure at the freezing point (practically 0° C.) was derived by the formula given above, and from this the pressure at 25° C. was obtained by the formula $P_t = P_f\,(1 + 0.00367\,t)$,[6] wherein P_t is the pressure at any given temperature (t).

Since ionization is usually more complete at high temperatures than at low ones, it was thought advisable to make some sample tests of osmotic pressure by determining the elevation of the boiling point. This was done for a limited number of solutions only. For this purpose the improved apparatus of Beckmann[7] was used. After the determination of P_f and P_b (*supra*), P_{25} was obtained by interpolation between them thus: $P_{25} = P_f + 25 \times 0.00367\,(P_b - P_f)$. The results show that the difference

[4] NERNST, W.: Theoretical chemistry, translated by C. S. Palmer, p. 123 *et seq.* 1895.

[5] BECKMANN: Zeitschr. Physik. Chem. **2**: 638. 1888.

[6] Simply the law of Gay-Lussac, which holds for osmotic pressures of weak solutions. NERNST: *op. cit.*, p. 134 *et seq.* Also OSTWALD, W., Outlines of general chemistry, translated by J. Walker, p. 128 *et seq.* 1895.

[7] BECKMANN: Zeitschr. physik. Chem. **8**: 223. 1891.

between the degree of dissociation at 0° C. and at 25° C. is so small as to be neglible for our present purpose.

The data obtained by these tests of the actual molecular conditions within these solutions are given in Table V. This is a supplement to the table given in the author's previous paper on this subject. In the first column are given the so-called percentage strengths of the solutions employed. In the second the solutions are designated by the letters previously used for that purpose (*loc. cit.*, p. 599). The next two columns contain the depressions of the freezing point and the elevations of the boiling point as directly observed. Then follow the two columns containing the osmotic pressures at the freezing and boiling points given in atmospheres. These numbers were obtained from Δ_f and Δ_b by the formulae given above. In the next two columns are given the pressures at 25° C., measured in centimeters of mercury, 1 being found from P_f by direct application of the law of Gay-Lussac, 2 by interpolation between P_f and P_b. The last column contains the pressures originally calculated by the assumption of complete ionization. They are introduced here for comparison.

It will be noted that there is a considerable range in the actual osmotic pressures of the different solutions whose calculated pressures are the same. This would be expected and is partially due to variations in the degree of ionization of the different salts according to their influence upon one another. It is also in part brought about by the fact that K_2HPO_4 dissociates completely only in very weak solutions. But this range of pressures lies entirely within the range of the pressure limits found for the several responses of the plant (*loc. cit.*, pp. 301, 306, 313). That is, the errors of calculation, while very large from a physical point of view, are not large enough to affect the physiological conclusions already expressed. This is on account of the comparatively low degree of sensitiveness of the organism with which we are dealing.

Discussion of the reasons for the curious variations from the calculated pressure manifested by these tests will be reserved

TABLE V.

PRESSURE DATA FOR NUTRIENT FLUIDS.

Per cent.	Solution	Δf	Δb	P_f (Atm.)	P_b (Atm.)	P_{25} (cm. Hg) (1)	P_{25} (cm. Hg) (2)	P (Calc.) (cm. Hg.)[8]
0.005	A	.023	....	.2776	....	23.0288	.....	16.19
	C	.012	.005	.1448	.285	12.0148	13.6701	
	D	.032	....	.3862	....	32.0475	.....	
0.1	A	.032	....	.3862	....	32.0475	.....	32.37
	C	.058	....	.7001	....	57.9861	.....	
	D	.041	....	.4949	....	41.0605	.....	
0.5	K	.154	.061	1.9088	3.477	158.3460	172.9608	161.86
	A	.124	....	1.5967	....	132.4809	.....	
	B	.155	....	1.8708	....	155.2300	.....	
	C	.165	....	1.9915	....	165.2392	.....	
	D	.185	....	2.2329	....	185.2728	.....	
1.0	K	.3	....	3.621	....	299.896	.....	323.71
	A	.235	.06	2.8364	3.42	235.3416	228.5578	
	B	.26	....	3.1382	....	260.3836	.....	
	C	.295	....	3.5606	....	295.4348	.....	
	D	.322	....	3.8865	....	322.4756	.....	
1.5	K	.4	.09	4.828	5.13	400.368	369.0180	487.59
	A	.32	....	3.8634	....	320.5604	.....	
	B	.381	....	4.5987	....	374.1936	.....	
	C	.433	....	5.2263	....	433.6408	.....	
	D	.465	.12	5.6125	6.84	465.7100	449.8644	
2.0	A	.415	.1	5.0007	5.7	414.9296	393.3380	647.42
	B	.46	....	5.543	....	459.9216	.....	
	C	.56	....	6.8444	....	567.9024	.....	
	D	.682	.15	8.2317	8.55	683.009	631.6588	

for a future paper. These data are published here merely as corroboration of the general conclusions already published. I wish to express my thanks here to Dr. Felix Lengfeld, of the Kent Chemical Laboratory of this University, for much kind advice and for the unrestricted use of the necessary facilities for such determinations as the above.

HULL BOTANICAL LABORATORY,
THE UNIVERSITY OF CHICAGO.

[8] See the author's previous paper, *loc. cit.*, pp. 301, 306.

BRIEFER ARTICLES.

INTRAMOLECULAR RESPIRATION.

THE experiment which is reported here failed in its original purpose, but the results which it did furnish seem to be worth reporting. The experiment was run in duplicate. Five grains of Japanese buckwheat, which had been previously soaked in distilled water for six hours, were placed in each of two eudiometers of 114^{cc} capacity. A piece of moist absorbent cotton was then placed loosely on the seeds, and the whole was secured in place by a cork with a groove in one side to admit of free circulation of the gases above and below. The volume of the seeds, cotton, and cork in the first eudiometer was 14.5^{cc}, and in the second 15.5^{cc}. The eudiometers were partly filled with mercury and inverted over a dish of the same metal. The column of mercury in no. 1 was 137^{mm}, and in no. 2 132^{mm} high. After reducing to standard pressure, no. 1 contained 65.41^{cc} and no. 2 contained 65.11^{cc} of atmospheric air.

The evolution of carbonic acid gas was quite rapid for the first few days. In forty-eight hours the volume of gases had increased so much that the column of mercury was entirely displaced and the gases had begun to escape through the dishes of mercury. This loss of gas seemed to invalidate the experiment, consequently the apparatus was set to one side until they could be again fitted up.

Some four weeks later it was decided to repeat the experiment with a smaller quantity of seeds; but before doing so 2^{cc} of strong caustic potash solution was introduced into each of the eudiometers to absorb any carbonic acid gas that might be present. An hour and ten minutes later it was found that the column of mercury in no. 1 had risen 215^{mm}, and in no. 2, 220^{mm} above the level of the dish, the temperature being 21° C. as at the beginning of the experiment. Thus, there was remaining in no. 1, after reducing to standard pressure, 32.49^{cc}, and in no. 2, 26.92^{cc} of gases. No. 1 contained, when the caustic potash solution was introduced, 99.5^{cc}, and no. 2, 98.5^{cc} of gases; hence no. 1 must have contained 67.01^{cc} of carbonic acid gas, of which, on the assumption that atmospheric air is 21 parts oxygen

and 79 parts nitrogen, 53.28^{cc} was evolved by intramolecular respiration, and no. 2, 71.58^{cc}, of which 57.91^{cc} came from the same source.

If 0.21 of the atmospheric air in the eudiometer at the beginning of the experiment was oxygen, and 0.79 nitrogen, then no. 1 must have contained 51.67^{cc} and no. 2 51.44^{cc} of nitrogen. Now at the close of the experiment, assuming that no other gas was present, no. 1 contained 32.49^{cc} and no. 2, 26.92^{cc} nitrogen; therefore 19.18^{cc} of nitrogen must have escaped from no. 1, and 24.52^{cc} from no. 2. On the assumption that the gases were completely diffused, the nitrogen that escaped from the first eudiometer must have carried with it 26.65^{cc}, and that from the second 38.62^{cc} of carbonic acid gas. This shows that from the seeds in the first eudiometer 79.93^{cc}, and in the second 96.53^{cc} of carbonic acid gas must have been evolved by intramolecular respiration.

To explain this apparent discrepancy between the two results, it should be stated that germination had not proceeded so far in no. 1 as in no. 2; in the former the sprouts on the seeds were from 2 to 4^{mm}, and in the latter from 4 to 6^{mm} in length. Slight decomposition had taken place in both eudiometers, but no fungus was visible in either.—T. C. Johnson, *West Virginia University*.

NOTES ON AQUILEGIA CANADENSIS Linn. AND A. VULGARIS Linn.

For several years I have had growing in my dooryard a patch each of our common eastern columbine and of the European or garden species, and have found them a fruitful source of pleasure and study. I wish to record a few of the more interesting observations. When the buds develop in the axils of the leaves, they at first stand erect, but soon begin to droop, and by the time the flowers begin to expand they hang completely inverted. As soon as the pollen has been shed and the ovaries have been fertilized, the flowers begin gradually to resume the erect position, and by the time the outer whorls have fallen the five-parted ovaries are standing erect, ready to mature, dehisce, and scatter the seeds. This rapid change in the position of the flowers is made possible by the great and rapid changes in the length and thickness of the peduncles. At first they are about one-fourth inch long and very slender; by the time the flowers have fallen and the ovaries are standing erect the peduncles have grown to be three to five inches long, and are thick rigid stems. This entire change takes place in about five days.

As soon as the petals separate at the apex, the five styles protrude and are ready to receive the pollen from other flowers, and before the anthers in the same flower are ready to shed pollen. The numerous stamens stand straight, around the pistil, except while the flowers first open and while the pistil is receiving pollen. At this time the outer ends of the filaments are bent outwards and away from the pistil at an angle of about 45°. As the innate anthers mature, however, and are ready to shed pollen, the filaments gradually assume the erect position. The pistils of the same flower by this time have had ample opportunity to receive pollen from other flowers. The stamens are from one-eighth to one-half inch shorter than the mature pistils. Hence close pollination is avoided by the protogynous condition of the flower, and by the stamens being shorter than and turned away from the stigmas.

The form and disposition of the spurs is quite different in the two species. In *A. Canadensis* the spurs are straight, while in *A. vulgaris* the outer end is curved inwards until it is again bent back on itself, forming an entire ring or circle. In *A. Canadensis* the spurs are longer and more slender and the tissues more tender. In both the nectary is located in the outer end of the spur, where it is represented by a hard nodule or gland. The common ruby-throated humming bird (*Trochilus colubris* L.), the tobacco and tomato sphinx moths (*Macrosila carolina* L. and *M. 5-maculata* Harr.) are common visitors to *A. Canadensis*, but I have never seen them visit *A. vulgaris*.[1] They take nectar by inserting the bill or tongue into the hollow of the spur, while the flower is still hanging in the inverted position. The body of the bird or insect is poised in the air by the rapid motion of the wings. This disturbs the air in the neighborhood violently, and so scatters the pollen widely in all directions.[2] In both species the Virginia carpenter-bee (*Xyocopa Virginica* L.) and a small bee (*Odynerus foraminatus* Sauss.) slit the tube of the spur, and take the nectar direct from the gland. Later, the honey bee (*Apis mellifica* L.) and a green bee (*Agapostemon radiatus* Say) enter these slits and secure the remaining nectar, but they do not make new slits themselves.—J. SCHNECK, *Mt. Carmel, Ill.*

[1] Perhaps for the reason that the curvature of the spurs of *A. vulgaris* renders it impossible for them to reach the nectar by the usual route.

[2] The inverted position of the flowers at this time renders it impossible for the pollen to fall into the open mouths of the spurs, and so be lost and useless to the flowers for pollination.

CURRENT LITERATRUE.

BOOK REVIEWS.

Guide to garden plants.[1]

THE intention of the writer has been to produce a book which will be of use to amateurs and also to those engaged professionally in horticulture. It deals with the description, cultivation, and propagation of the better known flowers, fruits, and vegetables suitable for growing in the British Islands. The subjects discussed are of such a comprehensive nature that it is quite impossible to expect that even a few of them should be treated in an exhaustive way within the limits of a single volume. A commendable feature—absent in other books on this subject—is a chapter devoted to the life history of plants, which is given in such a manner as to be readily understood by those not versed in technical language. The chapter on the description, cultivation, and propagation of the hardy fruits best suited to the climate of Great Britain gives little help to those in quest of such information in this country. Nearly a thousand pages are devoted to the description of the common plants in cultivation. The plants are arranged in their natural orders, cultural details are given in the majority of cases, and in this part of the work there is a similarity to what is found in the dictionaries of Paxton, Johnson, Nicholson, and Bailey. There is, of course, much in the book which will interest American readers; but, having been written for garden lovers in another part of the world, it would be a dangerous one to put in the hands of the uninitiated in this country, where not only the cultural details differ, but the species and varieties recommended as best would, in very many instances, be entirely unsuited to the conditions existing here.—G. W. OLIVER.

NOTES FOR STUDENTS.

ROSTOWZEW recommends two methods for drying plants which blacken readily.[2] One consists in using between the plants single layers of absorbent cotton 2^{cm} thick, covered with tough tissue paper, in a wire press, placed in a warm place. The other uses a perforate metal cylinder, to be covered with plants between sheets of filter paper held in place by a muslin jacket. The cylinder is covered with a lid and placed over a lamp. The plants dry in an hour or so.—C. R. B.

[1] WEATHERS, JOHN: A practical guide to garden plants and best kinds of fruits and vegetables. Large 8vo. pp. xii+1192. *figs. 163*. New York City: Longmans, Green, & Co., 1901.

[2] Flora **88**: 473–478. 1901.

NEWS.

JOSEPH Y. BERGEN, the author of well-known text-books on botany, has resigned his position in the English High School of Boston. With his family, he sailed on September 3 for Naples, Italy, where for the future he will make his home.— *Science.*

DR. EDWIN MEAD WILCOX has resigned his position at the Oklahoma Agricultural College and Experiment Station to accept the chair of biology in the Alabama Polytechnic Institute at Auburn. He entered upon his new duties the first of October.

MR. J. B. DANDENO, assistant in the Botanical Museum and in botany at Harvard University, has been appointed a teacher of botany in the St. Louis Normal and High School. DR. N. L. T. NELSON, formerly a fellow of the University of Chicago, has also been appointed to a similar position in the same institution.

DR. J. N. ROSE returned from his third Mexican journey about September 10, having been absent ten weeks. He has brought back a collection containing more than 1,100 numbers, made chiefly in the states of Mexico, Hidalgo, Vera Cruz, and Puebla, although work was also done in Jalisco and Morelos. Considerable collecting was done in the high mountains, especially about Pachucha and on Orizaba and Popocatepetl. Two trips were made to the latter mountain, and a very full set of its plants obtained, with careful aneroid records of all the higher species. The collection is especially rich in Oxalis, a genus which reaches a high development in Mexico.

A VERY SUCCESSFUL GATHERING of botanists was held in Geneva, Switzerland, on August 6, 7, and 8, when a program, that had been previously distributed, was closely carried out. About sixty members were in attendance, a surprisingly large number considering that no papers were read, and only a single topic was brought forward for discussion beside the details of organization.

Informal business and social matters occupied the first day. On the second day the congress formally opened in the botanical rooms of the University of Geneva, with Dr. Casimir de Candolle as honorary president, Professor R. Chodat as active president, and Dr. J. P. Lotsy as secretary. As announced in the preliminary circular, the question of establishing an international botanical journal, in which reviews of publications shall clearly indicate the merit of the work set forth, was taken up and warmly discussed in

all its phases. It was decided to found such a journal, contingent upon securing a sufficient number of subscriptions to maintain it. Dr. Uhlworm was chosen editor for a period of five years, and the new journal is to replace the *Botanisches Centralblatt*, which in consequence will be discontinued after the close of the present year.

During the afternoon the botanical gardens of the university and the famous DeCandolle herbarium were visited, and in the evening a brilliant reception was held, tendered to the congress by the city of Geneva. The last day of the meeting was given up to visits to the Barbey-Boissier herbarium at Chambésy and the gardens of M. Micheli at Jussy, with an elaborate banquet in the evening at the Eynard palace, tendered by the canton of Geneva. At this dinner the menu and the toasts had a strong international coloring, within European limits. After adjournment an excursion through the valley of the Saas to observe alpine plants was conducted by Professor Chodat.

The Americans in attendance at the congress were Mr. David G. Fairchild, of the United States Department of Agriculture; Mr. F. E. Lloyd, of Columbia University; Dr. D. S. Johnson, of Johns Hopkins University; Dr. H. von Schrenk, of the Missouri Botanical Gardens; Mr. and Mrs. W. Murrill, of Cornell University; and Dr. and Mrs. J. C. Arthur, of Purdue University. The meeting was fortunate in having pleasant weather; the local management was untiring in forwarding the interests of the meeting and in providing for the comfort and enjoyment of the members, and the opinion was unanimous that the gathering had been unusually enjoyable and successful. The next meeting of the Société Internationale de Botanique will be held in 1904 in Vienna, under the presidency of Professor Goebel, of Munich, Professor F. O. Bower, of Glasgow, being vice-president, and Dr. J. P. Lotsy, of Tjëbodas, Java, secretary.—J. C. ARTHUR.